An investigation into genetic improvement in reproductive efficiency in beef cattle through the unravelling of composite reproductive traits.

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Dissertation presented for the degree of Doctor of Philosophy in Agricultural Sciences in Animal Sciences at Stellenbosch University

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December 2007

I, the undersigned, hereby declare that the work contained in this dissertation is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree.

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Abstract

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by

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This study is a search for a quantifiable measure which estimates the genetic merit of female animals' breeding efficiency. For practical reasons, such a measure must be both simple and inexpensive to record, irrespective of the herd management strategy.

A literature investigation was undertaken to summarize breeding objectives for reproduction efficiency and to review different ways of expressing genetic reproduction efficiency. Traits to assess these in terms of the breeding objective, merits and requirements in terms of data collection are discussed.

During the lifetime of a cow events occur which influence her fertility. A distinction is made between component traits and aggregate traits: a component trait points to one event, while aggregate traits are composites of more than one event. Although all the traits discussed seem relevant for breeding value estimation, the practical application depends on the herd management system in use.

Age at first calving and days to calving are component traits that are easily and inexpensively measurable. Heritability estimates for the age at first calving were moderate. The heritability estimated for days to calving was 0.09.

Calving rate comes close to the overall breeding objective. The estimated heritability of calving rate is low (0.04), resulting in slow genetic improvement. Calving success was defined and investigated even though some constraints exist. A sire model proved that genetic variation exists for calving success on the underlying scale. The corresponding heritability estimate was 0.27.

Three categorical traits were defined. For stayability a sire variance of 0.41 was estimated with a heritabitity on the underlying scale of 0.27. The sire variances and heritabilities estimated for retention and calf tempo were high. Of the three traits, calf tempo is the one that reflects the true fertility of the bull's female progeny. Calf tempo was redefined as net breeding merit, a trait describing the retention of male animals and the reproductive performance of their female offspring. The obtained sire variances show that the trait is heritable and can be improved by selection. Net breeding merit gives an indication of the 'success' of sires in a given population. A heritability estimate of 0.20 was estimated on a data set comprising offspring of bulls older than nine years, but when offspring of all sires were included, heritability estimates of 0.08 and 0.11 for the Afrikaner and Bonsmara, respectively, were found.

Adjusting for young females was investigated by using the best linear unbiased estimate (BLUE) deviations to derive adjustment factors for herd level in order to predict performance for net breeding merit. Variation in the BLUE deviations occurred between all age class groups for the Afrikaner, whereas for the Bonsmara the variation between the BLUE deviations for the 3 year olds seems greater than the variation in the other age groups. It is suggested that the standardized curve for herd performance level derived from the BLUE deviations be used to adjust the phenotypic values of younger animals. This way the comparison between older and younger animals should be more valid.

In conclusion, reproductive traits are heritable and genetic improvement can be achieved through selection. Any economical viable beef enterprise should include at least one trait in their selection criteria that will improve the reproductive efficiency.

Opsomming

‘n Ondersoek na genetiese verbetering van reproduksie-doeltreffendheid in vleisbeeste deur die ontrafeling van saamgestelde reproduksie-eienskappe.

deur

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Hierdie studie is ‘n ondersoek na ‘n kwantifiseerbare maatstaf wat die genetiese meriete van vroulike diere se teeldoeltreffendheid beraam. Om praktiese redes moet so ‘n beraming sowel eenvoudig as goedkoop wees om te bepaal, onafhanklik van die kudde bestuurstrategie.

‘n Literatuurstudie is onderneem om die teeldoeleindes vir reproduktiewe doeltreffendheid op te som, sowel as om die verskillende wyses van genetiese reproduksiedoeltreffendheid beskrywing onder oë te neem. Verskeie eienskappe om hierdie beskrywings in terme van teeldoeleindes, meriete en dataversamelings-vereistes te raam, word bespreek.

Gedurende ‘n koei se leeftyd kom gebeurtenisse voor wat haar vrugbaarheid beïnvloed. Daar word onderskei tussen komponenteienskappe en aggregaateienskappe: ‘n komponenteienskap verwys na een gebeurtenis, terwyl aggregaateienskappe na samestellings van meer as een gebeurtenis verwys. Hoewel al die eienskappe wat bespreek word relevant voorkom, sal die praktiese toepassing afhang van die kuddebestuurstelsel in gebruik.

Ouderdom by eerste kalwing en dae tot kalwing is komponenteienskappe wat maklik en goedkoop bepaal kan word. Oorerflikheidsramings vir die ouderdom van eerste kalwing was matig. Die oorerflikheidsraming vir dae tot kalwing was 0.09.

Kalffrekwensie is baie na aan die oorkoepelende teeldoelwit. Die geraamde oorerflikheid vir kalffrekwensie is laag (0.04), wat stadige genetiese verbetering tot gevolg het. Kalfsukses is gedefinieer en ondersoek, hoewel enkele beperkings bestaan het. ‘n Vaar-model het aangetoon dat genetiese variasie ten opsigte van kalfsukses op die onderliggende skaal bestaan. Die ooreenkomstige oorerflikheidsraming was 0.27.

Drie kategoriese eienskappe is gedefinieer. Vir blyvermoë in die kudde is ‘n vaar-variansie van 0.41 geraam, met ‘n oorerflikheid van 0.27 op die onderliggende skaal. Die vaar-variansies en oorerflikhede wat vir retensie en kalftempo bereken is, was hoog. Van die drie eienskappe is kalftempo die een wat die ware vrugbaarheid van die bul se vroulike nageslag reflekteer. Kalftempo is herdefinieer as netto teelmeriete, ‘n eienskap wat die retensie van manlike diere en die reproduktiewe prestasie van hulle vroulike nasate beskryf. Die verkreë vaar-variasies wys dat die eienskap oorerflik is en verbeter kan word met seleksie. Netto teelmeriete gee ‘n aanduiding van die “sukses” van ‘n vaar in ‘n gegewe populasie. ‘n Oorerflikheidsraming van 0.30 is verkry op ‘n datastel bestaande uit die nageslag van bulle ouer as nege jaar, maar as die nageslag van alle vaars ingesluit is, was die oorerflikheidsraming onderskeidelik 0.08 en 0.11 vir die Afrikaner en Bonsmara.

Aanpassing vir jong vroulike diere is ondersoek deur gebruik te maak van die beste lineêre onpartydige beramings (BLUE) om korreksiefaktore vir die kuddevlak te verkry, ten einde die prestasie ten opsigte van netto teelmeriete te voorspel. Variasies in die BLUE afwykings het voorgekom tussen alle ouderdomsgroepe vir die Afrikaner, terwyl vir die Bonsmara die variasie tussen BLUE afwykings vir die 3-jaar oud diere groter was as vir die ander ouderdomsgroepe. Dit word voorgestel dat die gestandardiseerde kurwe vir kuddeprestasievlak wat afgelei word van BLUE afwykings gebruik word om die fenotipiesewaardes van jonger diere aan te pas. Op hierdie wyse behoort die vergelyking tussen ouer en jonger diere meer geldig te wees.

Ten slotte, reproduktiewe eienskappe is oorerfbaar en genetiese vordering is moontlik deur seleksie. Enige ekonomies lewensvatbare vleisbees-onderneming behoort ten minste een eienskap wat die reproduktiewe doeltreffendhied sal verbeter, in te sluit in seleksie kriteria.

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Acknowledgements

I would like to thank my husband, Jean, for his input and positive encouragement. Also my children, Jana, Hein and Andre who must have thought ‘vacation’ meant mom in front of the notebook.

My parents and siblings for their unequivocal belief in me.

Helena, without your belief and encouragement I would not have completed this study.

Dr J van der Westhuizen and Prof MM Scholtz and my other ex-colleagues at the ARC, Irene.

Prof SJ Schoeman for his just and supportive assessments.

Prof JB Van Wyk who acted as co-promoter.

The National Research Foundation for partially funding this study.

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Chapter 1

General Introduction

When humans began domesticating animals many centuries ago, they became aware of both heredity and variation. Domestication of wild animal species was a crucial achievement in the prehistoric transition of human civilization from hunting-and-gathering to agriculture. Humanity's close relationship with dogs reportedly began as far back as the end of the Ice Age. No one knows exactly how or why this first encounter took place. The earliest archaeological estimate indicates that it occurred in the late glacial period, approximately 14,000 years BC (Boessneck, 1985). Both Coppinger & Smith (1983) and Zeuner (1963) suggest that wild species which later became domesticated, started out as wild animals that followed humans for scrap waste as the humans moved from one camp to the next. Wolves were believed to have scavenged near human settlements or followed hunting parties. Wild cattle are suggested to have invaded grain fields and wild cats may have invaded grain stores while hunting for mice. The most recent evidence obtained by sequencing mitochondrial DNA of 67 dog breeds and wolves from 27 localities, however, indicates that dogs may have diverged from wolves over 100,000 years ago (Vila *et al.*, 1997; Vila, 2001).

The first domesticated livestock animal may have been the sheep, which was tamed around 9000 B.C. in Northern Iraq. Around 6500 B.C., domestic goats were kept in the same region and about 6000 B.C. the pig was domesticated in Iraq. By 5900 B.C. (and perhaps 3,000 years earlier) there were domesticated cattle in Chad, while independently about 5500 B.C. there were domesticated cattle in Iran. 3000 B.C. the horse was domesticated in Russia (Paszek *et al*., 1998; Giuffra *et al*., 2000; MacHugh & Bradley, 2001; Vila, 2001; Armelagos & Harper, 2005).

Domestication of livestock was performed through controlled mating and reproduction of captive animals which were selected and mated based on their behaviour and temperament. Animal breeders had to choose amongst animals at their disposal, those with distinctive favourable characteristics, which was then

propagated in future generations. Judging from cave paintings that have survived, selection was also applied to some qualitative traits such as coat colour and the absence or presence of horns. Without written records, there is no certain knowledge of the evolution of animal breeding practices, but written documents dating back more than 4000 years indicate that humans appreciated the significance of family resemblance in mating systems, recognized the dangers of intense inbreeding, and used castration to prevent undesirable males from reproducing. Progress in the performance of domesticated animals through these selection practices was very slow and it is believed that improvements were mainly due to animals adapting better to their environments (Price, 1984). Jacob was amongst one of the first recorded animal breeders that used observations to achieve set goals. By using his knowledge of coat colour patterns in animals, he acquired livestock from his uncle Laban (Gen 30:25-43).

The domestication of beef cattle initiated an opportunity for humans to apply their creativity to the formation of the modern beef cattle industry (Field & Taylor, 2002). The fact that people stayed in one place and domesticated animals to their benefit represented change in worldview. Land was divided into particular territories, collectively or individually owned, on which people raised crops and herds. More permanent housing, grain-processing equipment, as well ownership of domesticated herds connected people to places. The human mark on the environment was larger and more obvious following the rise of farming (Schultz & Lavenda, 1990).

Cattle play a unique role in human history. By some, they are considered as the oldest form of wealth. They have the ability to provide meat, dairy products and draft. The word "cattle" derives from the latin *caput*, head, and thus originally meant "one head" or "unit of livestock". The word is closely related to "chattel" (a unit of property) and to "capital" in the sense of "property." Cattle were originally identified by Carolus Linnaeus as three separate species. These were *Bos taurus*, the European cattle, including similar types from Africa and Asia; *Bos indicus*, the zebu; and the extinct *Bos primigenius*, the aurochs. In historical times, their range was restricted to Europe, and the last animals were killed by poachers in Masovia, Poland, in 1627. Breeders have attempted to recreate the original gene pool of the aurochs by careful crossing of commercial breeds, creating the Heck cattle breed (Kane, *et al*. 1997).

Virtually every function of every species shows variation, and these varying abilities in livestock led animal scientists to investigate and compare the efficiency and productivity of individuals. Understanding the relationship between chance and genetic expectations in the differences measured between individual animals is the key to comprehending the application of genetics to animal improvement. Scientists observed that the environment, as well as the heredity of favourable characteristics, plays a role in the breeding efficiency of livestock. To achieve genetic improvement, scientists endeavoured to identify and describe traits associated with efficiency and productivity. However, to implement genetic improvement, they firstly required accurate identification of each animal, its ancestors as well as its descendants, and secondly, measurements of performance for traits of importance.

For beef cattle, as is the case in many other domesticated livestock species, traits linked to reproduction efficiency are generally described as the most important factors contributing to efficiency and productivity (Meyer *et al*. 1990; MacNiel *et al*., 1994; Van der Westhuizen, 1997; Phocas *et al*., 1998). Many scientific publications on factors influencing efficiency in livestock have been published, describing suitable traits in the quest to improve overall reproductive efficiency. Reproductive efficiency in beef cows depends on many factors impacting on conception rate and survival of the offspring.

Reproduction in the female beef cow is complicated and subject to varying effects at different stages of the reproductive cycle. A cow must produce ova from the ovary that coincides with the exhibition of oestrous. After conception the cow has to provide the proper intra-uterine environment until the birth of the calf and then after calving a good maternal environment for her calf up to weaning. Thus, normal reproduction in beef cows involves the synchronization of many complicated physiological mechanisms that is further complicated by environmental influences as well as genetic ability for all mechanisms involved.

In beef cattle heifers, puberty is when the reproductive process commences. It occurs before mature body size is reached. Hormonal activity from the pituitary gland and subsequently from the gonads is responsible for the occurrence of the first oestrous. Via these organs, puberty is influenced by several factors of both hereditary and environmental nature. Once puberty has been reached, oestrous

occurs in non-pregnant cows in a rhythmic cycle called the oestrous cycle. Several pituitary and ovarian hormones are interrelated in controlling the oestrous cycle. Oestrous and ovulation are normally closely synchronized to increase the probability of fertilization. The cow has a double role to fulfil in the reproductive process. Firstly she has to produce viable ova and secondly, she must provide a proper uterine environment first for the sperm and later for the embryo and foetus during gestation.

Failure of any of the hormonal, environmental or hereditary mechanisms that influence and control the female reproductive cycle or gestation, will compromise reproduction and in some cases cause total reproductive failure. Environmental and genetic factors influencing reproductive efficiency in a herd will include the nutritional plane of the bulls and cows, the age of the animals, the general health of the herd, the libido of the bull, the quality of the bull's semen and the ability of the cow to conceive and maintain the pregnancy.

Improvement of fertility in a healthy herd, supplied with recommended levels of nutrition, can be obtained through improved management as well as improved genetic ability to reproduce through all stages of reproduction in beef cows. To achieve this goal, all events in the reproductive cycle of a cow should be recorded to detect changes in the reproductive pattern of the herd.

Figure 1.1 gives examples of the reproductive events in the lifespan of two cows within a herd. The first cow produced three calves over the time t_{1E} to t_{1X} (the time the cow was in the herd). Likewise, cow 2 produced three calves while in the herd, but over a shorter time span t_{2E} to $t_{2X.}$

Attempts to understand the genetics of a composite trait such as overall reproductive efficiency (ORE) in beef cattle females, can involve two approaches. The trait to be investigated could be the ORE itself or, alternatively, its constituent components. It is to be expected that these "component" traits will have different heritabilities. This invokes the possibility of concentrating on the most important components during selection and thereby possibly achieving a higher overall selection response. The first group of reproductive traits that can be identified from Figure 1.1, refers to an event in the reproductive cycle of the cow, and represent component traits. Calving ease (CE) is only indirectly related to reproductive performance in that a difficult calving may impact on the following conception. The

second group of traits, the aggregate traits, are compositions of more than one event in the reproductive cycle of the cow.

Cow 1	B---EH_1O_1---$J_1M_1P_1$------*$_1H_2O_2$-$J_2M_2P_2$------*$_2$---H_3O_3—J_3M_3------_H_4O_4-$J_4M_4P_4$------*$_3$-----H_5O_5—$J_5M_5P_5$----X
Time	t_{1E} ←----------→t_{1X}
Recordings	BW_o + BD_o BW_{c1}+BD_{c1} BW_{c2}+BD_{c2} BW_{c3}+BD_{c3}
Cow 2	B--E-H_1O_1-$J_1M_1P_1$-----*$_1$-H_2O_2-J_2M_2----_H_3O_3-$J_3M_3P_3$-----*$_2$-H_4O_4-$J_4M_4P_4$-----*$_3$-H_5O_5-J_5M_5-X
Time	t_{2E} ←----------→ t_{2X}
Recordings	BW_o + BD_o BW_{c1}+BD_{c1} BW_{c2}+BD_{c2} BW_{c3}+BD_{c3}

Where,

B	–	birth date of the cow	X	–	exit date
E	-	date of entering the herd	BW_o	–	cow's own birth weight
			BD_o	–	cow's own birth date
H_{1-n}	–	heat	$BW_{c1\ldots n}$	–	birth weights of calves
O_{1-n}	–	ovulation	$BD_{c1\ldots n}$	–	birth dates of calves
J_{1-n}	–	joining	t_{nE}	–	time of entry into herd
M_{1-n}	–	mating	t_{nX}	–	time when exiting the herd
P_{1-n}	–	pregnancy			
$*_{1-n}$	–	calving			
–	–	no calving			

Figure 1.1 Schematic representation of the reproductive cycle of two cows and at what time recordings are taken in the current South African Beef Cattle recording scheme.

It is clear that reproductive efficiency is a complex trait to identify. Sheldon & Dobson (2003) conclude that one of the challenges facing the beef cattle industry is the need to characterize reproduction. Although abundant research is available on beef cattle in confinement, reproductive responses to range management are few (Olson, 2005). In an attempt to supply the livestock industry with useful and reliable measures of reproductive efficiency, scientists have studied many different component traits. Some examples of these traits are calving interval (Brown *et al.,* 1954; Lindley *et al.,* 1958; Fagerlin, 1968; Schalles & Marlowe, 1969; Lòpez de Torre & Brinks, 1990), calving date (Lesmeister *et al.,* 1973; Bailey *et al*., 1985; Meacham & Notter, 1987; Marshall *et al.*, 1990; Buddenberg *et al*., 1990) and gestation length (Bourdon & Brinks, 1982; Azzam & Nielsen, 1987). These traits all observe only one measurement in the reproductive cycle, but can utilise many measurements of the same trait over the lifetime of a beef cow. In a further bid to quantify reproductive potential and efficiency in beef cattle cows, aggregates of above mentioned traits and others were defined to collectively describe more than one observation measured the

reproductive cycle over the lifetime of a beef cow. They include, amongst other traits, calving rate (Milagres *et al*., 1979; Mackinnon *et al*., 1990; Meyer *et al*., 1990), lifetime pregnancy rate (Morris & Cullen, 1994), calving success (Meyer *et al*., 1990; Johnston & Bunter, 1996; Van der Westhuizen *et al*., 2001) and calf survival (Milagres *et al.*, 1979).

Estimated breeding values (EBVs) for reproductive efficiency traits in females are difficult to estimate because the expression of the reproductive efficiency and potential of animals is often constrained by the management systems breeders employ (Notter, 1988; Notter & Johnson, 1988; Meyer *et al.*, 1990; Notter, 1995) and depends on the existing recording scheme. When managerial and nutritional conditions are optimal, most animals will reproduce, but in less favourable conditions, only those with the highest genetic merit for reproductive fitness will reproduce (Morris, 1980; Notter, 1995). Relatively few heritability estimates have been reported for female reproductive traits in beef cattle. These reports do, however, indicate that reproductive traits in beef cattle are heritable. Heritability estimates for cow reproductive traits are generally reported to be low (Davenport *et al.*, 1965; Dearborn *et al.*, 1973), but some studies from subtropical environments have reported moderate heritabilities (Deese & Koger, 1967; Cruz *et al.*, 1978; Thorpe *et al.*, 1981; Turner, 1982; Rust & Kanfer, 1998).

In the Southern tip of Africa, for perhaps as long as 10,000 years, the Bushmen or San were the only inhabitants. They are the last survivors of a Stone-Age culture. They were Hunter-Gatherers whose existence was governed by the seasons and the movements of the wild game. Then, about 4,000 years ago, the Hottentots or Khoi came south with their herds of cattle and sheep. They had semi-permanent settlements that they returned to each year, in which they lived in a clan system with a chief. Later the Bantu-speaking people came to the southern region, in search of grazing. This brought conflict with the Bushmen and Hottentots because the cattle competed with the antelope for grazing and water (Cameron & Spies, 1986).

Today, South Africa's national commercial cattle herd is estimated at 13.5 million, including various international breeds of dairy and beef cattle, as well as indigenous breeds such as the Afrikaner and Nguni. Locally developed breeds include the Drakensberger and Bonsmara. These breeds are systematically and

scientifically improved through breeding programs, performance testing and the evaluation of functional efficiency. The current recording scheme of the National Beef Cattle Improvement Scheme (NBCIS) of South Africa was implemented in 1959. In Phase A and B of this scheme, breeders keep pedigree records and weigh their animals at birth, weaning, yearling age and at 18 months. A few breeders weigh their cows at birth and weaning of the calves. Unfortunately, in South Africa, as most beef rearing countries of the world, very few herds measure any of the events in Figure 1.1. Instead, only the calving dates and weights at specified times of the calf's life are recorded. Reproduction information on cows can only be derived from birth notifications and weightings of their offspring. Thus, in the current national genetic evaluations done in South Africa for beef cattle, estimated breeding values (EBVs) for growth traits are reported with little indication as to the reproductive ability of the animals. This can lead to the assumption that genetic differences between animals for reproduction and fitness traits are trivial, a view often held by beef breeders.

Prior to performing a genetic evaluation of female reproduction traits, an objective has to be defined for the breeding program under consideration. For this study, the objective considered will be to maximise the number of calves born or weaned for a given number of cows in a herd under prevailing environmental and management conditions. This is a complex trait that has many components. While this is a function of the reproductive ability of each cow, it is also affected by the age structure of the herd as well as genetic and environmental factors on the bulls used. In the following, emphasis is placed on the performance of individual female animals only. The herd structure as well as between breed variation regarding the onset of puberty as well as the role of the bull used will, to a great extend, be disregarded. This is not because they are of lesser importance but merely to demarcate the study field for the dissertation.

Although heritability estimates for reproductive traits are generally low, selection for these traits is probably adequate using mixed model methodology (Meyer *et al*., 1991). Hetzel *et al*. (1989) used divergent selection in cattle for pregnancy rate and obtained genetic improvement, proving that by using the correct selection methods genetic progress can be achieved for reproductive ability. Even though the selection response per generation interval for traits describing reproductive efficiency is small

due to low heritability, selection for these traits will ensure the maintenance of the current genetic merit and guard against genetic decline in traits describing reproductive efficiency. Since the efficiency of reproduction is of cardinal importance in the overall productive efficiency of livestock, genetic decline can be ill afforded. This makes it viable to select for reproductive efficiency in any breeding program ensuring that, although selection response is slow, at least genetic maintenance is achieved and no genetic decline occurs.

In the following chapters an effort will be made to investigate different traits and methods whereby genetic gain for reproductive efficiency of female beef cattle in South Africa can be maintained or improved.

Chapter 2

Heritability estimates of female fertility traits in beef cattle: A literature review

Introduction

As described in chapter 1, reproduction in the female beef cow is complicated and subject to varying effects at different stages of the reproductive cycle. Normal reproduction in beef cows and bulls involves the synchronization of many complicated physiological mechanisms that is further complicated by environmental influences as well as genetic ability for all mechanisms involved.

The purpose of this literature investigation is to review different means to express the genetic reproduction efficiency of beef females. A number of auxiliary or index traits, following a chronological order of occurrence as described in Figure 1.1, are discussed to firstly assess them in terms of the breeding objective and secondly, their merits, shortfalls and requirements in terms of data collection.

Component traits

As described in the previous chapter, many events can be measured throughout the lifetime of a beef cow (Figure 1.1). Examples of these events are for instance the birth of the cow (B), first heat detection (H_1), first joining (J_1), calving($*_{1\text{-}n}$) etcetera. It is when one of these events occurs that a measurement can be taken to enable comparison between animals. From these measurements traits that influence the fertility of a cow can be identified. Since these traits are recorded at fixed events, they are referred to as component traits. In the following each component trait will be discussed briefly in a chronological order as they occur in the lifetime of a cow.

Time to first oestrous (TE)

For a fixed onset of the breeding season, time to first oestrous is defined as the number of days from the onset of the breeding season until a cow shows first oestrous. As such it can be measured on each animal at each parity. Evidence of a link between time to first oestrous and overall reproductive performance is vague. Clearly, an animal with a longer time to oestrous will on average (other things being equal) produce fewer calves in a given time. Estimates of genetic parameters indicate a favourable genetic relationship between scrotal circumference and age at puberty of heifers (Vargas et al., 1998). Selecting bulls for hip height will not adversely affect scrotal circumference but will have some detrimental effect on age of puberty in female progeny (Vargas et al., 1998).

Because the conditions under which South African farms are managed are mainly extensive, time to first oestrous cannot be measured easily as it involves close observation of the herd on a regular basis. Heritabilities for time to first oestrous for first, second and last parity were 0.05, 0.10 and 0.03, respectively (Azzam & Nielsen, 1987), however Vargas *et al*. (1998) estimated a high heritability of 0.42 for Brahman heifers. Heritability estimates for time to first oestrous are summarized in Table 2.1.

Number of services to conception (NSC)

Number of services to conception (NSC) is defined as the number of services needed for conception and is an indirect measure of one of the major time components in the reproductive cycle that shows large variation between animals, i.e. the time lapse between two calves. It requires the recording of each service, which is rarely available under natural service conditions. Heritabilities estimated for number of services per conception were between 0.03 and 0.64 with median 0.08 and standard deviation of 0.18 (Table 2.1), and indicate genetic variation among heifers for the number of services needed for conception at the first calving (Milagres *et al*., 1979; Hayes *et al*., 1992; Demeke *et al*., 2004; Choi *et al*., 2005, Azevêdo *et al.,* 2006; Chang *et al.,* 2006; Heringstad *et al.,* 2006 & Nishida *et al.,* 2006). Nishida *et al*. (2006) found that number of services to conception is a more heritable trait in heifers than in cows with different parities. Repeatability of number of services to

Table 2.1 Summary of literature estimates of heritabilities (h^2) and repeatabilities (r^2) for different female reproductive traits *(1 of 9)*

Trait	Author	Breed	Parity	Comment	h^2	r^2
Time to 1st oestrous	Azzam & Nielsen (1987)		1st		0.05	
			2nd		0.10	
			3rd		0.03	
	Vargas *et al*. (1998)	Brahman			0.42	
No of services/conception	Milagres *et al.* (1979)			Puberty heifers	0.64	
	Hayes *et al*. (1992)	Holsteins			0.03	0.07
	Demeke *et al*. (2004)	Crosses			0.08	
	Choi *et al*. (2005)	Hanwoo			0.20	
	Azevêdo *et al*. (2006)	Nelore			0.05	0.09
	Chang *et al.* (2006)			Censored threshold-linear	0.04	
	Heringstad *et al*. (2006)			Threshold	0.03	
	Nishida *et al.* (2006)		1st	RRM	0.15	
			6th		0.04	
			10th		0.22	
			1st	Multiple trait	0.13	
Pregnancy rate	Dearborn *et al.* (1973)				0.09	
	Weigel & Rekaya (1999)	Holstein		Minnesota	0.01	
				California	0.01	
	Burrow (2001)	Composite			0.04	
	Goodling *et al*. (2005)	Dairy			0.10-0.26	
	MacNiel *et al.* (2006)			Trait of female	0.07	
				Trait of service sire	0.02	

Table 2.1 *Continued (Part 2 of 9)*.

Trait	Author	Breed	Parity	Comment	h^2	r^2
Heifer pregnancy	Doyle *et al.* (1996)				0.21	
	Evans *et al.* (1999)				0.14	
	Doyle *et al.* (2000)				0.21	
	Eler *et al.* (2002)				0.57	
	Silva *et al.* (2003b)	Nelore			0.30	
	Silva *et al.* (2005)				0.52	
	Minick-Bormann *et al.* (2006)	Angus		Threshold	0.13	
Gestation length	Burfening *et al.* (1978)	Simmental			0.48	
	Bourdon & Brinks (1982)			Male calves	0.36	
				Female calves	0.37	
	Azzam & Nielsen (1987)		1st		0.41	
			2nd		0.45	
			3rd		0.36	
	Wray *et al.* (1987)	Simmental		Sire model	0.37	
				Mat. grandsire	0.09	
	Azevêdo *et al*. (2006)	Nelore			0.12	0.22
	Crews (2006)	Charolais			0.64	
Days to calving	Meyer *et al.* (1990)	Hereford			0.05	0.22
		Angus			0.08	0.10
		Zebu crosses			0.09	0.18
	Johnston & Bunter (1996)				0.11	
	Burrow (2001)	Composites			0.07	
	Rust & Van der Westhuizen (2002)	Bonsmara			0.09	
	Forni & Albuquerque (2005)				0.06 to 0.13	

Table 2.1 *Continued (Part 3 of 9)*.

Trait	Author	Breed	Parity	Comment	h^2	r^2
Age at first calving	Harwin *et al.* (1969)				0.14	
	Lesmeister *et al.* (1973)				0.09	
					0.11	
	Bourdon & Brinks (1982)				0.07	
	Hanset *et al*. (1989)	Belgian Blue			0.03	
	Lôbo (1998)	Zebu			0.29	
	Rust & Kanfer (1998)	Afrikaner			0.27	
		Dr'berger			0.30	
	Van der Westhuizen *et al.* (2001)	Multibreed composites			0.40	
	Martínez-Velázquez *et al*. (2003)	*Bos taurus*			0.08	
	Nilforrooshan & Edriss (2004)	Holstein			0.09	
	Donoghue *et al*. (2004a)				0.06	
	Cerón-Muñoz *et al*. (2004)	Nelore		Brazilian	0.19	
				Colombian	0.13	
	Demeke *et al.* (2004)	Crosses			0.44	
	Yilmaz *et al*. (2004)	Angus			0.26	
	Forni & Albuquerque (2005)				0.06 to 0.08	
	Roughsedge *et al*. (2005)	Aberdeen Angus			0.22	
		South Devon			0.05	
		Limousin			0.26	
		Simmental			0.17	
	Azevêdo *et al*. (2006)	Nelore			0.21	

Table 2.1 *Continued (Part 4 of 9)*.

Trait	Author	Breed	Parity	Comment	h^2	r^2
Calving date	Harwin *et al.* (1969)					0.14
	Lesmeister *et al.* (1973)					0.10
	Itulya (1980)	Hereford			0.09	
	Bourdon & Brinks (1982)				0.07	
	Bailey *et al.* (1985)					0.12
	Johnson & Notter (1987)			Simulation	0.04	
	Meacham & Notter (1987)		1st calving		0.17	
			2nd calving		0.07	
	Azzam & Nielsen (1987)		1st parity		0.09	
			2nd parity		0.03	
			Last parity		0.17	
	Smith *et al.* (1989)				0.09	
	López de Torre & Brinks (1990)				0.16	0.26
	Buddenberg *et al.* (1990)		1st parity	Excluding open	0.20	
			2nd parity	cows	0.04	
			Last parity		0.03	
			1st parity	Including open	0.39	
			2nd parity	cows	0.13	
			Last parity		0.00	
	Rege & Famula (1993)	Hereford			0.16	0.23
	Notter *et al.* (1993)	Angus			0.18	
	MacNiel & Newman (1994)			Direct	0.23	
				Maternal	0.06	
				Permanent Env.	0.09	
	Van der Westhuizen *et al.* (2001)	Multibreed composites			0.04 / 0.06	

Table 2.1 *Continued (Part 5 of 9)*.

Trait	Author	Breed	Parity	Comment	h^2	r^2
Calving ease	Klassen *et al.* (1990)				0.02	
					0.05	
	Cubas *et al.* (1991)			Direct	0.07	
				Maternal	0.20	
	Naazie *et al.* (1991)	Synthetic		Raw	0.36	
				Transformed	0.47	
				Binary scale	0.26	
	Notter *et al*. (1993)				0.07	
					0.38	
	Kriese *et al*. (1994)				0.11	
				Binary scale	0.09	
	Varona *et al.* (1999a)			Linear	0.18	
				Threshold	0.23	
	Carnier *et al.* (2000)	Italian	1st	Direct	0.19	
		Piedmontese		Maternal	0.09	
			2nd	Direct	0.10	
				Maternal	0.11	
			2nd + later	Direct	0.08	
				Maternal	0.05	
	Bennet & Gregory (2001)	Composites		Trait of calf	0.43	
				Trait of Dam	0.23	
	Wiggans *et al.* (2003)			Direct	0.09	
				Maternal	0.05	
	Eriksson *et al.* (2004)	Charolias		Direct	0.11-0.16	
		Hereford		Maternal	0.07-0.12	
	Roughsedge *et al*. (2005)	South Devon		Direct	0.19	

Table 2.1 *Continued (Part 6 of 9)*.

Trait	Author	Breed	Parity	Comment	h^2	r^2
Calving ease *(cont.)*	Roughsedge *et al*. (2005) *(cont.)*			Maternal	0.11	
				Permanent Env.	0.03	
		Limousin		Direct	0.13	
				Maternal	0.07	
				Permanent Env.	0.31	
		Simmental		Direct	0.35	
				Maternal	0.09	
				Permanent Env.	0.02	
		Aberdeen Angus		Direct	0.26	
				Maternal	0.08	
				Permanent Env.	0.06	
	Gutiérrez *et al*. (2007)	Asturiana de los Valles		Direct	0.19	
				Maternal	0.14	
Calving interval	Brown *et al.* (1954)				0.01	
	Lindley *et al.* (1958)				0.07	
	Plasse *et al.* (1966)					0.03
	Fagerlin (1968)				0.03	
	Schalles & Marlowe (1969)				0.03	0.02
	Bailey *et al.* (1985)					-0.05
	Meacham & Notter (1987)				0.04	
	Hanset *et al*. (1989)	Belgian Blue			0.03	
	López de Torre & Brinks (1990)				-0.03	0.14
	Lôbo (1998)				0.14	0.15
	Van der Westhuizen *et al.* (2001)	Multibreed composites			0.01	
	Olori *et al*. (2002)				0.04	

Table 2.1 *Continued (Part 7 of 9)*.

Trait	Author	Breed	Parity	Comment	h^2	r^2
Calving interval *(cont.)*	Demeke *et al.* (2004)	Crosses			0.08	0.14
	Roughsedge *et al*. (2005)	Aberdeen Angus			0.09	
		South Devon			0.13	
		Limousin			0.04	
		Simmental			0.10	
	Azevêdo *et al*. (2006)	Nelore			0.05	0.05
	Gutiérrez *et al*. (2007)	Astur. d l Valles			0.12	
Days Open	Hayes *et al*. (1992)	Holsteins			0.05	0.10
	Demeke *et al.* (2004)	Crosses			0.04	0.14
	Oseni *et al*. (2004)	Holsteins			0.03-0.06	
	Goodling *et al.* (2005)				0.03-0.07	
	Goyache *et al*. (2005)		1st		0.09	
			2nd		0.20	
	Chang *et al.* (2006)			Censored threshold-linear	0.04	
Calving rate	Milagres *et al.* (1979)			Incl open cows	0.02	
				Excl open cows	0.45	
	Mackinnon *et al.* (1990)			Female	0.11	
				Male	0.08	
	Meyer *et al.* (1990)	Hereford			0.07	
		Angus			0.02	
		Zebu crosses			0.17	
	Yilmaz *et al*. (2004)	Angus			0.11	
	Guerra *et al*. (2006)	Multi breed		Linear	0.06	
				Threshold	0.15	
				Logistic	0.13	

Table 2.1 *Continued (Part 8 of 9)*.

Trait	Author	Breed	Parity	Comment	h^2	r^2
Calving success	Meyer *et al.* (1990)	Hereford			0.08	
		Angus			0.02	
		Zebu crosses			0.08	
	Johnston & Bunter (1996)				0.11	
	Van der Westhuizen *et al.* (2001)	Multibreed composites			0.03	
	Goyache *et al.* (2003)	Asturiana de Vos			0.03 – 0.08	
	Donoghue *et al*. (2004a)				0.03	
Calf survival	Milagres *et al.* (1979)			Binary scale	0.64	
				Adjusted h^2 (van Vleck, 1972)	1.25	
	Cubas *et al.* (1991)	Angus		Direct	0.04	
				Materna	0.09	
	Guerra *et al*. (2006)			Linear	0.05	
				Threshold	0.16	
				Logistic	0.19	
Length of productive life	Martinez *et al.* (2004)				0.05 to 0.15	
	Roughsedge *et al*. (2005)	Aberdeen Angus			0.13	
		South Devon			0.10	
		Limousin			0.08	
		Simmental			0.03	

Table 2.1 *Continued (Part 9 of 9)*.

Trait	Author	Breed	Parity	Comment	h^2	r^2
Ovulation rate	Echternkamp *et al* (1990)			Pubertal heifers	0.07	
	Gregory *et al* (1990a)			DFREML	0.03	
	Gregory *et al* (1990b)				0.07	
	Van Vleck *et al* (1991)			Pubertal Heifers	0.16	
	Van Tassell *et al*. (1998)			REML	0.07	
				Transform LM	0.18	
				Threshold	0.17	
Multiple births	Syrstad (1984)		1 st	Binomial scale	0.01	
			3 - 5		0.04	

conception were estimated as between 0.07 and 0.09 (Hayes *et al*., 1992; Azevêdo *et al.,* 2006).

Pregnancy rate (PR)

Pregnancy rate (PR) is defined for each cow in each year as a 1 for a successful pregnancy and a 0 otherwise. It's a binary trait and requires pregnancy detection on the herd. The relationship of pregnancy rate with age appears to be correlated with the body condition score decrease at breeding in older cows. This supported the inclusion of body condition score at breeding in the statistical model when analysing pregnancy rate (Renquist *et al*., 2006). Amundson *et al*. (2006) reported a change in pregnancy rate when the average minimum temperature and temperature-humidity index equal or exceeded certain levels.

Heritability estimates for pregnancy rate are summarized in Table 2.1. Heritabilities estimated for pregnancy rate were between 0.01 and 0.26 with median 0.04 and standard deviation of 0.09 (Dearborn *et al*., 1973; Weigel & Rekaya, 1999; Burrow, 2001; Goodling *et al*., 2005 & MacNeil *et al*.,2006). Results of Morris & Cullen (1994) generally showed a negative genetic correlation with yearling (-0.30) or lifetime pregnancy rate (-0.29). Recording of this trait is time consuming and expensive (Morris & Cullen, 1994). From this trait, another trait, namely lifetime pregnancy is defined as the number of pregnancies of a cow divided by the number of mating years.

Heifer Pregnancy (HP)

Heifer pregnancy is a binary trait defined as the probability of a heifer conceiving and remaining pregnant to 120 days of gestation, given that she was exposed at breeding (Doyle *et al.,* 1996; Evans *et al.,* 1999). In Table 2.1 literature estimates of parameters are summarised. Heritabilities estimated for heifer pregnancy were between 0.13 and 0.57 with mode 0.21 and standard deviation of 0.18 (Doyle *et al.,* 1996; Evans *et al.,* 1999; Doyle *et al.,*2000; Eler *et al.,* 2002; Silva *et al.,* 2003b; Silva *et al.,* 2005 & Minick Bormann *et al.,* 2006). Eler *et al.* (2002) estimated a heritability of 0.57 (using Method R) concluding that heifer pregnancy can be used to select heifers with higher probability of being fertile. However, it is

mainly recommended for selection of bulls because the accuracy of prediction is generally higher for bulls due to more information. Silva *et al.* (2003b) estimated a genetic correlation between hip height and probability of pregnancy of Nelore heifers as 0.10 ± 0.01 indicating that selection for growth measured by hip height is not such a strong antagonism to precocity of heifers at 14 months age.

Perry *et al.* (2007) indicated that the logistic regression of the size of the ovulatory follicle at the time of insemination and pregnancy rate in beef heifers is curvilinear with a predicted maximum pregnancy rate at a follicle size of 12.8mm.

However, it seems that the effect of nutrition on the reproductive performance of heifer calves remains crucial. For heifers born from dams that received a nutritional supplement, pregnancy rates were greater and a greater proportion calved in the first 21 days of the heifers first calving season (Martin *et al*., 2007), stressing the importance of correctly identifying the contemporary groups when attempting genetic analysis of heifer pregnancy.

Gestation length (GL)

Gestation length (GL) certainly exhibits variation between animals. Being a time component in the reproductive cycle, this will then also impact on overall reproductive performance of the animal. However, this effect will be insignificant, as the variance in GL is rather small relative to the variation in calving interval. Also, it requires the observation and recording of two dates, namely at service and at calving. The former, particularly, is rarely available under natural service conditions. Heritabilities estimated for heifer pregnancy were between 0.09 and 0.64 with mode 0.36 and standard deviation of 0.16 (Burfening *et al*., 1978; Bourdon & Brinks, 1982; Azzam & Nielsen, 1987; Wray *et al*., 1987; Azevêdo *et al*., 2006 & Crews, 2006).

Bourdon & Brinks (1982) used paternal half-sib analysis and a least-squares procedure to compute a heritability of 0.36 for bulls and 0.37 (Table 2.1) for heifers for gestation length. These were similar to those compiled by Andersen & Plum (1965), but were lower than the heritability of 0.48 estimated by Burfening *et al.* (1978) for Simmentaler cattle. Heritabilities for gestation length in first, second and last parity were 0.14, 0.45 and 0.36, respectively (Azzam & Nielsen, 1987). Using Herderson's Method III, heritability for gestation length was estimated for

Simmentaler cattle as 0.37 from the sire variance and 0.09 from the maternal grandsire variance (Wray *et al.*, 1987). Crews (2006) estimated a high heritability of 0.64 for gestation length (Table 2.1).

Days to calving (DC)

Days to calving was computed by Meyer *et al.* (1990) and Johnston & Bunter (1996) as the interval in days between the first joining date for cows and subsequent calving for cows under natural mating conditions. Days to calving is a continuous variable if the calving percentage is 100%. Johnston & Bunter (1996) suggest a penalty for non-calvers of 21 days added to last calvers in joining management groups. Days to calving and calving date give the same information when cows which were compared went into breeding the same day. In field-data, especially in a between herd analysis, this is almost never the case. Heritability estimates for days to calving are summarized in Table 2.1. Heritabilities estimated for days to calving were between 0.05 and 0.13 with mode 0.09 and standard deviation of 0.03 (Meyer *et al.*, 1990; Johnston & Bunter, 1996; Burrow, 2001; Rust & Van der Westhuizen, 2002 & Forni & Albuquerque, 2005).

Meyer *et al.* (1990) fitted an animal repeatability model, including an animal effect, other than additive genetic, as an additional random effect for each animal. This effect was assumed to be identically, independently distributed and not correlated with the animals' additive genetic effects. Meyer *et al.* (1990) estimated pooled heritabilities for days to calving of 0.05 for Hereford, 0.08 for Angus and 0.09 for Zebu crosses, with repeatabilities of 0.22, 0.10 and 0.18, respectively. Pooled heritability estimated by Johnston & Bunter (1996) was 0.11 for subsequent days to calving. Johnston & Bunter (1996) estimated a heritability of 0.11 for calving success, and a very high genetic correlation (r_g = -0.97) between days to calving and calving success. Rust & Van der Westhuizen (2002) estimated a comparable heritability of 0.09 for the indigenous South African Bonsmara breed. Forni & Albuquerque (2005) concluded in a study of genetic correlations between days to calving and other reproductive and weight traits in Nelore cattle that the use of days to calving in the selection criteria may promote favourable correlated responses in age at first mating and consequently higher gains in sexual precocity.

Age at first calving (AFC)

A reduced age at first calving (other effects being equal) will increase the number of calves within the herd. Nunez-Dominguez *et al*. (1991) investigated the economic efficiency of lifetime production of beef heifers calving first at two or three years of age. They concluded that the economic efficiency was higher for heifers calving first at two years than heifers calving first at three years of age, regardless of the culling policy. This supported the finding by Marshall *et al*. (1990) that an earlier first calving date was economically more efficient because a greater proportion of their annual production cycle was in a productive mode, diluting increased maintenance cost as a fraction of all cost.

Age at first calving is available without additional recording effort as the birth date of the cow and its first calving date is generally known. The biggest disadvantages are, firstly, that age at first calving deals only with one component in the reproductive life of a cow. Secondly, it is recorded only on heifers, while later calvings do not add more information. Thirdly, in a variable seasonal environment, as is the case in South Africa, the age at first calving is more of a management decision than the expression of genetic merit. Because of the seasonal nature of production differences due to management strategies, the resulting variance in reproductive performance will not reflect true genetic differences.

Heritability estimate for early calving was found to be low (0.14) in the study of Harwin *et al.* (1969). In a study done by Lesmeister *et al.* (1973), heifers calving earlier initially tended to calve earlier throughout the remainder of their productive lives, however, repeatability estimates from this study were low (0.092 and 0.105). A low heritability estimate (0.07) was calculated by Bourdon & Brinks (1982) who found the correlations between age at first calving and growth traits consistently negative, indicating a favourable relationship between breeding values for growth and early reproduction. Gutiérrez *et al*. (2002) found that the genetic relationship between age at first calving and type traits were, in general, non-favourable.

Nilforooshan & Edriss (2004) estimated a heritability of 0.09 for age at first calving and found that age at first calving significantly affected traits like milk yield, fat yield, fat percentage as well as the lifetime of Holstein cows. Rust & Kanfer (1998)

reported much higher heritabilities for two indigenous South African beef cattle breeds of 0.27 and 0.30, respectively. Literature estimates of parameters are summarised in Table 2.1. Heritabilities estimated for age at first calving were between 0.03 and 0.44 with mode 0.09 and standard deviation of 0.11 (Harwin *et al.*, 1969; Lesmeister *et al.*, 1973; Bourdon & Brinks, 1982; Hanset *et al.*, 1989; Lôbo, 1998; Rust & Kanfer, 1998; Van der Westhuizen *et al.*, 2001; Martinez-Velázques *et al.*, 2003; Nilforrooshan & Edriss, 2004; Donoghue *et al.*, 2004a; Cerón-Muñoz *et al.*, 2004; Demeke *et al.*, 2004; Yilmaz *et al.*, 2004; Froni & Albuquerque, 2005; Roughsedge *et al.*, 2005 & Azevêdo *et al.*, 2006).

Calving date (CD)

Calving date is defined as the day of the year on which the cow calves (Notter, 1995). It allows comparison between cows when joining has the same duration and starts on the same date. However, no distinction can be made among cows calving in the same 21-day period (one oestrous cycle) (Notter, 1988). To overcome this period, cows can be classified into 21-day calving groups (Lesmeister *et al.,* 1973; Bailey *et al*., 1985; Marshall *et al.*, 1990). The problem when analysing such a trait is what to do with cows that do not calve in a specific year. A procedure to calculate penalties for open cows was proposed by Notter & Johnson (1988) calculating the predicted value of the trait for non-calvers using threshold theory. This method assumes a normal distribution of the trait and a predicted value for all non-calvers (x) as given by the equation:

$$x_2 = \bar{x}_1 + (z / p[1-p])\, s$$

With p = proportion of cows calving

z = the height of the ordinate at the truncation point (t) of the normal distribution

s = $\{s^2_1 p / [\, p\text{-}z\, (\, z / p - t]\}^{½}$ the standard deviation of the trait;

s^2_1 = observed variance amongst calves

t = truncation point

This method was used by several researchers (Buddenberg *et al.,* 1990; Meyer *et al.,* 1990) to calculate the value for non-calvers.

In the study by Meacham & Notter (1987) first and second calving date records of animals that calved at the age of two years for the first time were used in variance component estimation. Calculations were performed using the nested analysis of variance procedure of SAS (1985).

Heritabilities (h^2) were estimated as:

$$h^2 = 4\sigma^2_s / (\sigma^2_s + \sigma^2_e),$$

where σ^2_s = sire variance

σ^2_e = error variance

with assumptions that differences in heritability are due to common environment and dominance is zero.

Genetic correlations (r_G) were estimated from sire components of variance and covariance. The pooled heritability estimates were 0.17 for first calving and 0.07 for second calving. The genetic correlation between first and second calving dates was 0.66 and using calving date as selection criterion to improve reproductive fitness seems plausible. Heritability estimates for calving date are presented in Table 2.1. Heritabilities estimated were between 0.00 and 0.39 with mode 0.09 and standard deviation of 0.09 (Itulya *et al.*, 1980; Bourdon & Brinks, 1982; Johnson & Notter, 1987; Meacham & Notter, 1987; Azzam & Nielsen, 1987; Smith *et al.*, 1989; López de Torre & Brinks, 1990; Buddenberg *et al.*, 1990; Rege & Famula, 1993; Notter *et al.*, 1993; MacNeil & Newman, 1994 & Van der Westhuizen *et al.*, 2001). In contrast to the study by Azzam & Nielsen (1987), Buddenberg *et al.* (1990) found that the heritability estimates declining from first to last parity. Repeatabilities for calving date were estimated by Harwin *et al.* (1969), Lesmeister *et al.* (1985), López de Torre & Brinks (1990) and Rege & Famula (1993) respectively (Table 2.1). Gutiérrez *et al*. (2002) estimated that type traits and calving date appeared to be genetically independent with correlations ranging from 0.00 to -0.125.

Due to large climatic differences between the different regions of South Africa the start and duration of joining differ between breeders within the same breed, with the result that this trait is not appropriate for use in a South African National Analysis.

Calving ease (CE)

Calving ease (CE) will have an indirect effect on the overall reproductive efficiency (ORE) in that the calving interval following a difficult calving will tend to be extended. In order to distinguish between more than two categories for ease of calving, the trait requires the observation of calving and can therefore only be obtained from well-controlled production environments.

Sire is a significant source of variation for calving ease score in 2-year old and mature dams (Burfening *et al.*, 1979). The correlation of sire EPDs (estimated progeny difference) between calving ease for 2-year old and 3-year old dams was estimated as 0.46 and 0.21 (Table 2.1) compared to mature dams. Kriese *et al.* (1994) found that average genetic correlations between male and female 320-day pelvic width, pelvic height and pelvic area were large and positive, concluding that male and female pelvic traits are mainly under the same genetic control, but are correlated traits rather than the same trait.

Notter (1988) summarized direct heritabilities for calving ease ranging from 0.07 to 0.38 and for maternal effects ranging from 0.07 to 0.18. Cubas *et al.* (1991) found that the maternal variance for calving ease was much larger than the variance for the direct effect of the sire. Heritabilities estimated for calving ease were between 0.02 and 0.47 with mode 0.19 and standard deviation of 0.13 (Klassen *et al.*, 1990; Cubas *et al.*, 1991; Naazie *et al.*, 1991; Notter *et al.*, 1993; Kriese *et al.*, 1994; Varona *et al.*, 1999a; Carnier *et al.*, 2000; Bennet & Gregory, 2001; Wiggans *et al.*, 2003; Eriksson *et al.*, 2004; Roughsedge *et al.*, 2005 & Gutiérrez *et al.*, 2007). Estimates of genetic correlations for calving ease in different parities were high, but variance components and heritabilities were clearly heterogeneous over parities Carnier *et al.*, (2000).

The repeatability of calving ease was estimated in Canadian Holsteins as 0.06 to 0.08 with heritability estimates ranging from 0.02 to 0.05 (Klassen *et al.,* 1990). Meijering & Postma (1985) found a positive correlation between direct and maternal grandsire genetic merits for ease of calving in Dutch Red and Whites. Genetic correlations of daily gain were positive with direct calving difficulty and negative with maternal calving difficulty indicating that specific selection strategies must be taken due to the existence of this antagonistic relationship (Albera *et al*., 2004). The genetic

and phenotypic correlation between calving ease as a trait of the dam and pelvic dimensions were low, whereas the correlations between calving ease and dam weight at calving were moderate. As a trait of the calf, calving ease was highly correlated genetically with calf birth weight, but the phenotypic correlations were moderate (Naazie et al., 1991). Bennett & Gregory (2001) found that the direct effects of two year old calving difficulty score seemed to be more closely tied to birth weight than were maternal effects.

Calving interval (CI)

Calving interval (CI) is a trait that combines many of the above component traits. As such it has similarities with the following aggregate traits. CI is the time between two successive calvings. Thus, it is only available for cows from the second parity onwards. Because it is based only on the period between two calvings, it can be computed with minimal data recording. However, this recording will be at a loss of reproductive information for the first parity as well at the end of a cow's life span when no calf is born. Analysing calving interval is problematic since it is only available for cows that calve again and should therefore rather be treated as a censored trait. Because of the relatively low estimated heritability for calving interval, Bourdon & Brinks (1983) and Meacham & Notter (1987) concluded that calving interval did not appear to be a useful criterion with which to improve female reproduction. Marshall *et al*. (1990) found calving interval to be a biased measure under a limited breeding season and culling of open cows. However, when no fixed breeding season is observed and cows are allowed to calve throughout the year, calving interval is useful as a measure of reproductive ability (Bourdon & Brinks, 1983; Meacham & Notter, 1987).

Heritability estimates for calving interval (Table 2.1) are low and were estimated between -0.03 and 0.14 with mode 0.03 and standard deviation of 0.04 (Brown *et al.,* 1954; Lindley *et al.,* 1958; Plasse *et al.,* 1966; Fagerlin, 1968; Schalles & Marlowe, 1969; Bailey *et al.,* 1985; Meacham & Notter, 1987; Hanset *et al*., 1989; López de Torre & Brinks, 1990; Lôbo, 1998; Van der Westhuizen *et al.,* 2001; Olori *et al*., 2002; Demeke *et al.,* 2004; Roughsedge *et al*., 2005; Azevêdo *et al*., 2006 & Gutiérrez et al., 2007). Repeatability estimates of calving interval between second and third and

third and fourth years of age were found to be negative by Bailey *et al.* (1985) and Werth *et al.* (1996). However other authors reported low positive repeatabilities ranging between 0.02 and 0.15 (Plasse *et al*., 1966; Schalles & Marlowe, 1969; de Torre & Brinks, 1990; Lôbo, 1998; Demeke *et al.,* 2004 & Azevêdo *et al*., 2006). In Nelore cattle repeatabilities estimated for calving interval suggested that female culling based on the first calving interval is not accurate and there is a risk of culling animals with probable good reproductive efficiency (Azevêdo *et al*., 2006).

Gutiérrez *et al*. (2002) estimated favourable genetic correlations between type traits and calving interval, but since the correlations with calving date and age at first calving was either non-favourable of independent, constructing a type trait index to improve reproductive performance was small.

Days Open (DO)

Days open is defined in the literature as the interval from calving to next conception. Days open and calving interval is usually influenced by similar factors, since gestation length is a fixed interval (Hafez & Hafez, 2000). Estimated heritabilities for days open vary between 0.03 and 0.20 with a mode of 0.04 and standard deviation of 0.05 (Hayes *et al*., 1992; Demeke *et al.,* 2004; Oseni *et al*., 2004; Goodling *et al.,* 2005; Goyache *et al*. 2005 & Chang *et al.,* 2006). Demeke *et al*. (2004) estimated a repeatability of 0.14 for days open in crosses between Boran and Friesian and Boran and Friesian, Jersey crosses.

The genetic correlations estimated for days open in different parities were between 0.90 and 1.00, indicating that the genes affecting days open are substantially the same over parities (Goyache *et al*., 2005). Goyache *et al*. (2005) found a substantial permanent environment in younger cows for days open. Genetic correlations were found to be high and positive between days open and calving interval and negative and low between days open and gestation length and calving date, respectively.

Aggregate traits

While component traits refer to an event in the lifetime of a cow, aggregate traits are composites of more than one event. For the aggregate traits to be measured more than one event must occur and be measured.

Calving rate (CR)

Calving rate is a lifetime measure of the reproduction performance of a cow. It is defined as the number of calves born divided by the number of opportunities a cow has had to produce a calf. If opportunities are defined as the number of years in which the cow could have produced a calf, calving rate comes close to the overall breeding object (ORE) as defined above and, therefore, seems to be a useful trait when aiming to improve female reproductive performance of a herd. Estimated heritabilities for calving rate vary between 0.02 and 0.45 with a median of 0.11 and standard deviation of 0.12 (Milagres *et al.,* 1979; Mackinnon *et al.,* 1990; Meyer *et al.,* 1990; Yilmaz *et al*., 2004 & Guerra *et al*., 2006).

For cows with one parity, calving rate is a binary trait while it becomes more continuous as the number of parities increases. Being a trait that is an average of the (different) number of parities of each cow, calving rate does have a variable accuracy depending on the number of parities involved. This will definitely have to be considered in genetic evaluation by using a different residual variance for each calving rate record. Furthermore, herd entry and exit dates have to be recorded, as well as the pregnancy status of a cow on exiting the herd to be able to compute this trait correctly. This information is rarely available in the South African recording system. In Table 2.1 literature estimates of parameters are summarised.

Lifetime pregnancy rate

From the trait pregnancy rate a lifetime trait, namely lifetime pregnancy rate, can be defined as the number of pregnancies divided by the number of mating years for an animal (Morris & Cullen, 1994). A favourable genetic correlation exists between lifetime pregnancy rate and the pubertal traits scrotum circumference and age at first oestrus (Morris & Cullen, 1994). This trait is, as previously mentioned, time consuming and expensive to record.

Calving success (CS)

Calving success can be defined for each cow in the herd for each year. Calving success is, therefore, a binary trait with either ones for successful calvings or zeros when no calf was born. Apart from calving, entry and exit dates of each cow have to be available. Secondly, as with calving rate, information on the pregnancy status of the cow on exiting the herd is crucial. Although very similar to CR, this trait has multiple measurements (a measurement with each parity) for each cow and is evaluated as a repeatability trait in genetic analysis.

Johnston & Bunter (1996) estimated a heritability of 0.11 for calving success. Deese & Koger (1967) estimated moderate to high heritabilities for calving success (it is called calving rate and is defined as a binary trait: pregnant – 1 & other – 0). Heritabilities of binary data were adjusted to a normal basis with the equation suggested by Dempster & Lerner (1950):

$$h^2 = h^2_b \; p[p-1] / z^2$$

With: h^2_b = heritability estimated in binomial scale

h^2 = heritability in normal scale

p = frequency of non-calvers

z = height of the distribution at the threshold point

Simulation studies have, however, shown that this adjustment tends to overestimate on the underlying scale when the frequency is low and the heritability is high (Van Vleck, 1972). Milagres *et al.* (1979) estimated heritabilities for early calving success rate at 2-years of age, defined as calf born = 1 and no calf = 0, from paternal half sib correlations using Harvey (1976). Heritability estimates for calving success are summarized in Table 2.1 and vary between 0.02 and 0.11 with a mode of 0.08 and standard deviation of 0.03 (Meyer *et al.,* 1990; Johnston & Bunter, 1996; Van der Westhuizen *et al.,* 2001; Goyache *et al.,* 2003 & Donoghue *et al*., 2004a).

Calf survival (CSU)

The survival of a calf after birth is clearly a component of overall reproductive efficiency. It is a binary trait and available for each parity of each cow that calved.

Calf survival was defined by Milagres *et al.* (1979) as dependent variables calf born alive (1) or dead (0). It's similar to the trait calving rate as defined by Deese & Koger (1976), Milagres *et al.* (1979) and Mackinnon *et al.* (1990), and calving success as defined by Meyer *et al.* (1990). A heritability estimated from paternal half sib correlations was 0.64 on the binary scale, with the adjusted heritability calculated with the equation proposed by Van Vleck (1972) greater than one (1.25±0.35). Heritability estimates for calving survival are summarized in Table 2.1 and vary between 0.04 and 1.25 with a median of 0.18 and standard deviation of 0.48 (Milagres *et al.,* 1979; Cubas *et al.,* 1991 & Guerra *et al*., 2006).

Lifetime production (LPL/O)

Lifetime production was defined by Martinez *et al.* (2004) as the length of productive life of a cow given the opportunity measured as days between first calving and disposal. Heritability estimates for LPL/O ranged from 0.05 to 0.15 (Table 2.1). Martinez *et al.* (2004) concludes that selection for LPL/O can be successful in a breeding program, but that genetic progress will be relatively slow due to the low magnitude of heritability as well as the extended generation interval. Heritability estimates for lifetime production are summarized in Table 2.1 and vary between 0.03 and 0.15 with a median of 0.09 and standard deviation of 0.05 (Martinez *et al.,* 2004 & Roughsedge *et al*., 2005).

Negative correlations were found between most productive traits measured in dairy cattle in the first three lactations and lifetime production (Sölkner *et al.*, 2003).

Other traits

To measure these other traits, an event or number of events do not have to occur or be measured.

Ovulation rate (OR) to improve twinning

Increasing the twinning rate is seemingly a promising path to increase the number of calves produced by a cow in her lifetime. This will increase the overall

productive performance in a herd. Heritability estimates for ovulation rate are summarized in Table 2.1 and large differences are documented among breeds. Van Vleck *et al.* (1991) found genetic correlations between twinning rate and ovulation rate of between 0.38 and 1.00. This suggests that selection for twins can be done indirectly by measuring ovulation rate in oestrous cycles of pubertal heifers (Echternkamp *et al.*, 1990; Van Vleck *et al.*, 1991; Van Tassell *et al*., 1998). Echternkamp *et al.* (1990) pointed out that repeated measurements of ovulation rate on the same animal should increase the effective heritability of mean ovulation rate. Genetic correlations between incidence of multiple births in first and subsequent parities were estimated by Syrstad (1984) as 0.52 – 0.64 and those among parities two to five were between 0.70 and 0.84. Bilateral ovulations (one corpus lutuem on each ovary) are preferred since it results in twin pregnancies that show decreased dystocia and increased calf survival (Cushman *et al*., 2005). Cushman *et al*. (2005) found ovulation rate of one ovary was negatively correlated with ovulation rate of the same ovary in the previous cycle, but positively correlated with the contra lateral ovary in the previous cycle. They conclude that bilateral ovulations may be an economically important trait, which will respond to selection.

While there may be circumstances where twinning is desirable, the study by Gregory *et al.* (1990a,b) documented some serious constraints to increased twinning rate in beef cattle that should be alleviated before the potential of twinning can be exploited as a production technology to reduce the cost of beef production. These constraints include increased dystocia, reduced calf survival at birth and a reduced re-breeding performance of cows that gave birth to twins.

Under the extensive South African farm conditions, twinning is usually considered as a disadvantage due to the extra management input twin-bearing cows often require.

Summary

It is clear that the environment and resources available to animals play a major part in the decision on which traits to be measured, recorded and used as predictors of female fertility in a herd. When resources are in abundance and the environmental conditions optimal, an intensive beef cattle management system can be followed.

However, the scarcer the resources and less favourable the environmental conditions become, the more extensive beef cattle management systems will be.

Intensive systems of beef cattle management, allows measurement and recording of a large number of traits, since the animals are kept in smaller camps and it is easier to observe them. The number of traits that can be measured will decline as the intensity level of the management systems becomes more extensive. It becomes virtually impossible in extensive beef cattle management systems to observe and handle the animals on a daily basis. To record the number of services per conception in an intensive management system is feasible, but an attempt to measure this trait in semi-intensive and extensive management systems is virtually impossible since animals are usually kept in large camps on feeding pastures or natural grazing and are not handled every day. This will restrict the number of measurements that can be recorded. The intensity of the farming management system will thus determine the traits associated with female fertility that can be measured as well as the frequency with which these traits can be measured.

To measure and record traits such as pregnancy rate and ovulation rate require specialised techniques, apparatus and know-how. The expertise of a professional would be acquired to observe and measure such traits. For this reason it will be more expensive to measure, thus limiting its opportunity to be measured and recorded notwithstanding the intensity level of the management system.

A problem that often occurs in the recording of female fertility traits is a lack of precise bookkeeping or absence of key measurements when recording the traits. In South Africa, the greatest disadvantage in the past was that the herd entry and exit dates of cows as well as the pregnancy status at herd entry and herd exit was seldom recorded by most breeders. If recorded, it was not noted in the national database. Proper management bookkeeping and national recording is of the utmost importance in the recording of all traits. For some traits such as calving interval, gestation length and number of services per conception, the standard error is likely to be small. For traits like days to calving and age at first calving and other traits, it is likely to be larger. Thus, for some traits more than others, when bookkeeping is not precise, it can have a large influence on the prediction of genetic merit of animals as well as the selection response in generations to follow.

Although all the fertility traits discussed in this chapter, to a greater or lesser degree seems to be describing the female reproductive performance of a cow herd, few traits describe lifetime reproductive performance. Most of the traits focus and define a specific measurement (event) or measurements (events) that happen during the lifetime of the cow's reproductive cycle (Table 2.2), and the information recorded from these measurements is then expanded to determine which animals are reproductively more efficient. Two traits that consider only one event in the lifetime production of the cow is age at first calving and heifer pregnancy. Age at the fist calving or heifer pregnancy of a cow is taken as a predictor of a female's ability to reproduce efficiently although it is based on only one event measured very early in her life. This makes them very easy measurements to record and they can be recorded in any environmental management system, from very extensive up to intensive management systems.

Calving rate, as defined by Milagres *et al.* (1979), express the number of calves of a cow divided by the number of opportunities a cow had to calve. For this trait as well as for lifetime productive life two counts are needed, namely the total number of calves of a cow in her lifetime as well as all the opportunities she had to do so. These traits qualify as traits that can be recorded effortlessly for all different management systems. All the other traits defined by various researchers in the past as discussed in this chapter, must be recorded and measured repeatedly during specific events as they occur over the lifetime of a cow.

It is clear from the description of each trait as well as from the summary of all traits given in Table 2.2 why all traits are not suitable for different environments. Due to the extensive or intensive nature of the management, the recording of some measurements may be difficult to accomplish and control. The intensity of the management system will limit the traits that can be measured for each management system. It will also limit the frequency with which some traits can be recorded. All breeders will ultimately employ the management system that best suits the resources that are available to them. To implement a measurement of reproductive efficiency on a national basis successfully, a trait describing the reproductive efficiency of female beef cattle must be applicable and executable by all prevailing management intensity systems. For a trait to be a successful candidate as indicator of the national

Table 2.2 Summary of reproduction traits in female beef cattle and what and when measurements needs to be taken.

Trait	Life time	Each Parity	B	E	J_1	O_1	H_1	H_{1n}	P_1	$*_1$	CE_1	CS_1	J_n	O_n	H_n	H^{nn}	P_n	$*_n$	CE_n	CS_n	….	x
AFC	**x**	**-**	**x**							**x**												
TE	**-**	**x**			**x**		**x**						**x**		**x**							
GL	**-**	**x**					**x**			**x**					**x**			**x**				
NSC	**-**	**x**					**x**	**x**		**x**					**x**	**x**		**x**				
PR	**-**	**x**							**x**								**x**					
HP	**x**								**x**													
CSU	**-**	**x**										**x**								**x**		
CE	**-**	**x**									**x**								**x**			
CI		**x**								**x**								**x**				
CR	**x**	**-**		**x**						**x**								**x**				**x**
CS	**-**	**x**		**x**						**x**								**x**				**x**
DC	**-**	**x**			**x**					**x**			**x**					**x**				
OR	**-**	**x**				**x**								**x**								
CD	**-**	**x**								**x**												
LPL/O	**x**			**x**						**x**								**x**				**x**

AFC - Age at first calving
TE - Time to 1st oestrous
GL - Gestation length
NSC - No. of services/conception
PR - Pregnancy rate
HP - Heifer Pregnancy
CSU - Calving success
CE - Calving ease
CI - Calving interval
CR - Calving rate
CS - Calving survival
DC - Days to calving
OR - Ovulation rate
CD - Calving date
LPL/O Length of productive life
B,E,J,O,H,P,x Figure 1.1

fertility of female beef cattle, the trait must be easy to record, with as little as possible bookkeeping, cheap to measure and applicable in all intensity levels of management systems.

As described in the introduction, reproduction in the female beef cow is complicated and is subject to varying effects at different stages of the reproductive cycle. Normal reproduction in beef cows involves the synchronization of many complicated physiological mechanisms that is further complicated by environmental influences as well as genetic ability for all mechanisms. In Figure 2.1 an illustrative representation is given of the interaction between environmental effects, the genotype of the dam and calf and how this influence the traits described above. Figure 2.1 also aim to illustrate how the different traits describing reproductive efficiency in the beef cow interact with and influence one another.

Conclusion

Although all the traits discussed in this chapter seem applicable for breeding value estimation, the practical application is not feasible under different management systems. The times at which measurements for various traits have to be taken are shown in Table 2.2. It is evident that four traits consider the lifetime production of the animal as one measurement, *viz.* age at first calving, heifer pregnancy, calving rate and lifetime productive life. All other traits must be measured repeatedly over the lifetime of the cow. It is clear that the beef cattle management system of each herd will, to a great extent, determine which traits can be measured for fertility. The cost involved to measure some traits may influence breeders when making a decision whether to measure a trait or not. When considering a trait to be analysed in a National analysis, it would probably have to be a trait that can be measured in most management systems at a low cost. The more extensive the system, the fewer component traits can be measured and incorporated as variables in a genetic model.

Since South African beef cattle production tends to rely more on semi-extensive and extensive systems, traits to consider will be calving rate, lifetime productive life, calving success, calf survival, days to calving, age at first calving, heifer pregnancy rate, calving date, calving ease and calving interval. It should be noted that inclusion

of these traits, given all the constraints, may jeopardize the reliability of breeding values. Furthermore, model specification for these traits is usually difficult. It is recommended that joining dates, herd entry and exit dates and the pregnancy status of animals exiting the herd be recorded.

From Figure 2.1 it is clear that most traits will be influenced or will influence other traits as defined in this chapter. In most cases, improvement in one of the traits will bring about improvement in other traits describing reproductive efficiency. Breeders should be aware of the interactions between traits when deciding on a trait to use in national evaluations when aiming to improve the reproductive efficiency of a beef cow herd.

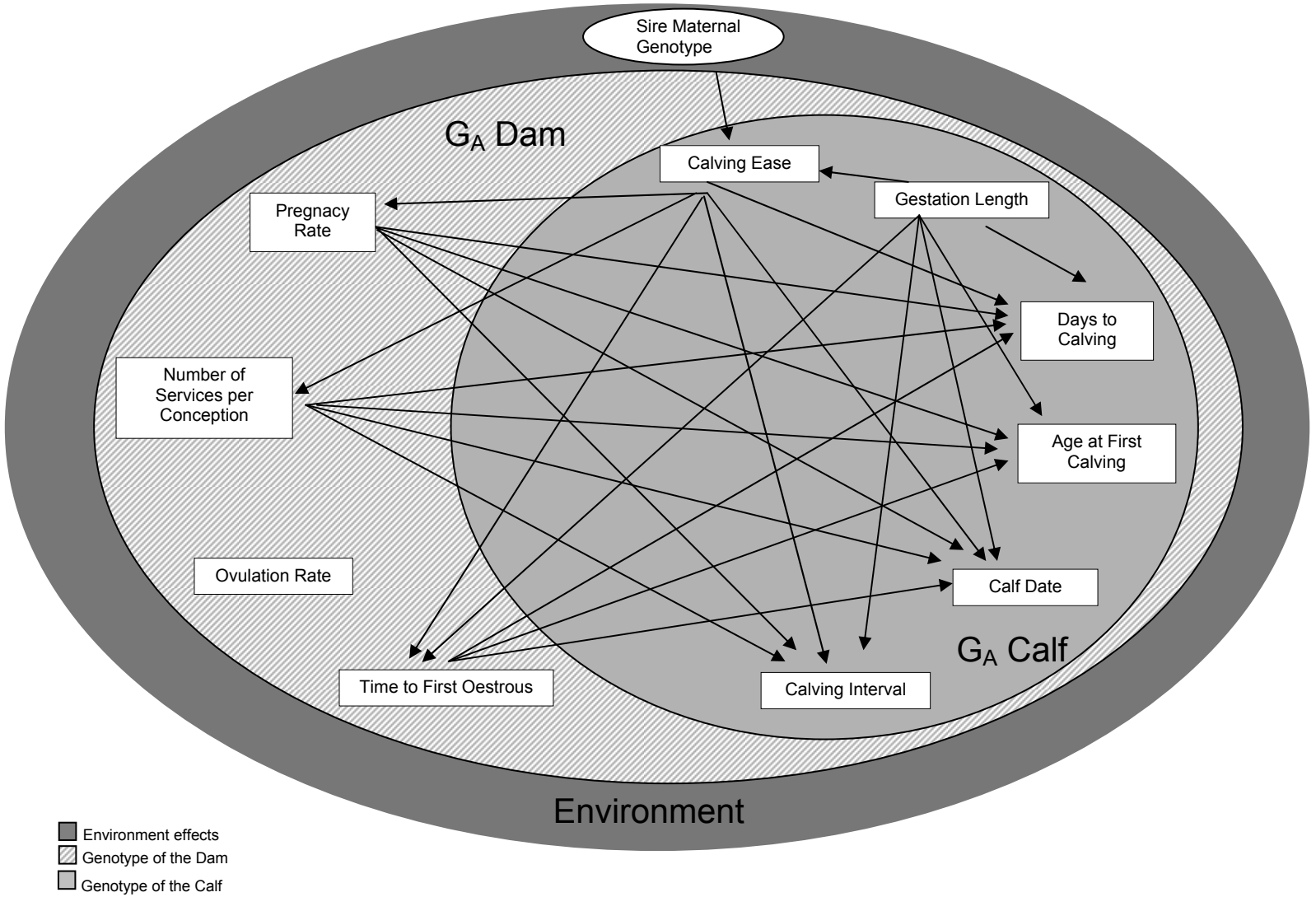

Figure 2.1: Illustrative representation of the interaction between environmental effects, the genotype of the dam and calf influencing all the traits described in this chapter as well as the interaction between these traits.

Chapter 3

Component traits: Age at First Calving and Days to Calving

Introduction

From the conclusions drawn in Chapter 2, it is clear that there is no complete satisfactory measure of female reproduction efficiency that can be applied to beef cattle in South Africa. Some possibilities are discussed to measure reproductive ability, but most of these traits are not without shortcomings and some restrictions when describing the overall reproductive efficiency (ORE) in a beef cattle herd. Most of the traits discussed are either too difficult to measure in all management intensity levels, some are too expensive to record, or some do not fully address the complexity of the trait of female reproduction efficiency. However, a few traits were identified that warrant further investigation as possible measures of reproduction efficiency in the South African system. If some of these traits can be applied in future, more accurate selection decisions can be made to achieve a favourable selection response for reproduction efficiency in beef cattle herds.

From the conclusions of Chapter 2, two component traits, age at first calving (AFC) and days to calving (DC), were defined as traits that can be used as possible indicators of female reproduction efficiency. Parameters estimated in the literature are given in Table 2.1. Early age at first calving increases the overall lifetime efficiency of a beef cow (Pope, 1967). A reduced age at first calving will increase the number of calves born for a given number of animals and decrease the generation interval. This will increase the genetic selection response to selection for reproduction efficiency. Meacham & Notter (1987) and Buddenberg *et al.* (1990) concluded that genetic variation exists for age at first calving and the trait could be used in sire selection as a measure of daughter reproductive ability.

Nilforooshan & Edriss (2004) investigated the effect of age at first calving on total lifetime and productive life as well the effect of age at first calving on first-lactation yields in Holstein cows. They concluded that reducing the age at first calving

has a significant positive effect on milk yield as well as productive life, but that reducing age at first calving below 21 month of age had a negative effect on yields of milk and milk fat. Silva *et al*. (2005) estimated a favourable correlation of -0.32 between age at first calving and heifer pregnancy. A study by Cerón-Muñoz *et al.* (2004) on age at first calving was done to determine if there is a genotype x environment interaction in Holstein cattle from Brazil and Colombia. They estimated a genetic correlation between Brazilian and Colombian Holsteins of 0.78, concluding that differences in ranking of sires were consistent with a genotype x environment interaction.

Age at first calving is easy to record in all management intensity levels and is measured only once during the lifetime of a female animal with no additional expenses to the breeder. It is available without additional recording effort, as the birth dates of all animals as well as the first calving dates of heifers are generally known in all intensity levels of management. However, since a long time interval from birth is needed to record age at first calving, accurate information on young females will only be available after the recording of their first calf. In areas and countries where management systems are more extensive to semi-extensive, this will be on average at the age of 2½ years. Due to this, as well as relatively low heritability estimates (Table 2.1), it is important to record all available information on relatives when selecting for age at first calving.

The interval in days between the first joining or exposure date of the bulls to the cow herd and the subsequent calving of cows under natural mating conditions was defined by Meyer *et al*. (1990) and Johnston & Bunter (1996) as a trait indicating female fertility. Days to calving, as fertility indicator, have some favourable characteristics. Firstly, it excludes some of the variation in the reproductive performance of cows that is due to management decisions of the breeder. Secondly, days to calving is a reasonably easy trait to measure.

Meyer *et al*. (1990) considered days to calving closely related to the trait calving date. Days to calving differs from calving date in that it requires the added information of the first joining date. It is a trait that can be easily recorded in all intensity levels of management systems where natural mating is practised. Furthermore, recording days to calving is with no additional expense to the breeder.

Calving date is defined as the day of the year on which the cow calves (Notter, 1995). It allows comparison between cows when joining has the same duration and starts on the same date. No distinction can, however, be made between cows calving in the same 21-day period (one oestrous cycle) (Notter, 1988). To overcome this problem, cows can be classified into 21-day calving groups (Lesmeister *et al*., 1973; Bailey *et al*., 1985; Marshall *et al*., 1990). The problem when analysing days to calving and calving date is what to do with cows that do not calve in a specific year. For calving date, a procedure to calculate penalties for open cows was proposed by Notter & Johnson (1988) calculating the predicted value of the trait for non-calvers using threshold theory.

For days to calving, penalties for cows not calving in a specific season were introduced by Johnston & Bunter (1996). They proposed a penalty for non-calvers added to the last calver in a joining management group. They proposed adding 21 days penalty to cows not calving in a breeding season. These 21 days were added to the last calving date from any cow in the same herd with similar joining date. Johnston & Bunter (1996) found a favourable genetic correlation between calving success and days to calving as well as similar heritability estimates for the two traits, suggesting that the two traits were similar, with the ability of days to calving to distinguish between early and late calvers as an added advantage. They also estimated high genetic correlations for days to calving records from different parities. This allowed them to treat records from different parities as repeated records from the same trait.

Donoghue *et al.* (2004a) examined the relationship between days to calving and two measures of fertility in AI data, i.e. calving to first insemination and calving success. The authors estimated correlations that indicate a strong, negative relationship between days to calving and both measures of fertility in AI data. They concluded that selecting for animals with a genetic ability to have a shorter days to calving interval, will lead to correlated improvement in both the interval from calving to first insemination and calving success (Donoghue *et al*., 2004a).

The genetic correlation between days to calving and scrotal circumference was estimated by Forni & Albuquerque (2005). They estimated the correlation as low and negative (-0.10) and the correlation between days to calving and age at first calving

as high and positive, predicting that selection for days to calving in beef cattle may promote favourable correlated responses to age at first mating with higher gains in sexual precocity.

Mercadante *et al.* (2003) concluded in a study that selection for body weight promoted high consistent weight and height responses both at yearling and later ages, without compromising the reproductive performance of the cows with respect to days to calving and calving success.

In South Africa the recording of the joining date of bulls has never been compulsory. Whenever it was recorded by selected breeders, it was not recorded in the National data base of NBCIS. Thus, investigating the trait days to calving, holds some challenges since no verified data sources are available. The Bonsmara Breeder Society is the largest beef cattle society in South Africa. The Bonsmara breed is a beef breed indigenous to South Africa and it is considered adapted to semi- and extensive management systems. Through the years the society has requested its breeders to keep mating lists to be submitted to the office of the Bonsmara Society on a regular basis. The data had, however, never been recorded electronically, but stored at the offices. Previously no study had been undertaken utilizing these data.

The aim of the study is to evaluate the merit of the component traits, age at first calving and days to calving as indicators of female reproductive efficiency.

Material and Methods

Data of three indigenous beef breeds of South Africa, the Afrikaner, Drakensberger and Bonsmara were used in studying the two traits age at first calving and days to calving. For the investigation of age at first calving, data from purebred Afrikaner and Drakensberger females of herds participating in the NBCIS were extracted from the Integrated Registration and Genetic Information System (INTERGIS). Cows calving for the first time in the period 1976 to 1996 were considered if age at first calving was less than 60 months. The age of 60 months was chosen arbitrarily. It was reasoned that the registration of a first calf for a cow older than the age of 5 years (± 60 months) was probably due to non-registration of previous calves or a managerial decision taken for specific animals. After editing, the

data set for the Afrikaner breed consisted of 9 723 records and that of the Drakensberger of 14 750 records. The general statistics of the Afrikaner and Drakensberger data is presented in Table 3.1. All pedigree information available from the INTERGIS for the Afrikaner and Drakensberger breeds were used in the analyses.

Table 3.1 General statistics of the data used in the age at first calving investigation

	N	Min	Max	Avg	SD
		Age (months)			
Afrikaner	9 723	22	59	42.6	8.2
Drakensberger	14 750	18	60	41.5	9.5

The distribution of the observations for both the Afrikaner and Drakensberger breeds is presented in Figures 3.1 and 3.2, respectively. It is clear that the management decisions as to when to breed heifers for the first time has a big influence on the distribution of the observations for age at first calving. Two distinct peaks can be observed, indicating that generally breeders have fixed breeding seasons in which the heifers are bred. This reflects a managerial decision based on the environment and nutritional level the animals are exposed to.

The GLM procedure of SAS (1996) was used to determine the operational models that best describe the data for age at first calving. The final statistical model for both the Afrikaner and Drakensberger breeds included herd x year x season concatenations as fixed effects. Table 3.2 indicates the number of levels for each effect for each of the breeds.

Table 3.2 Number of levels for fixed and random effects included in the final genetic analysis of age at first calving for the Afrikaner and Drakensberger breeds

Factor	Type	Number of levels	
		Afrikaner	Drakensberger
Herd x year x season	F	1 695	2 759
Animal	A	168 835	118 275

F = Fixed

A = Random

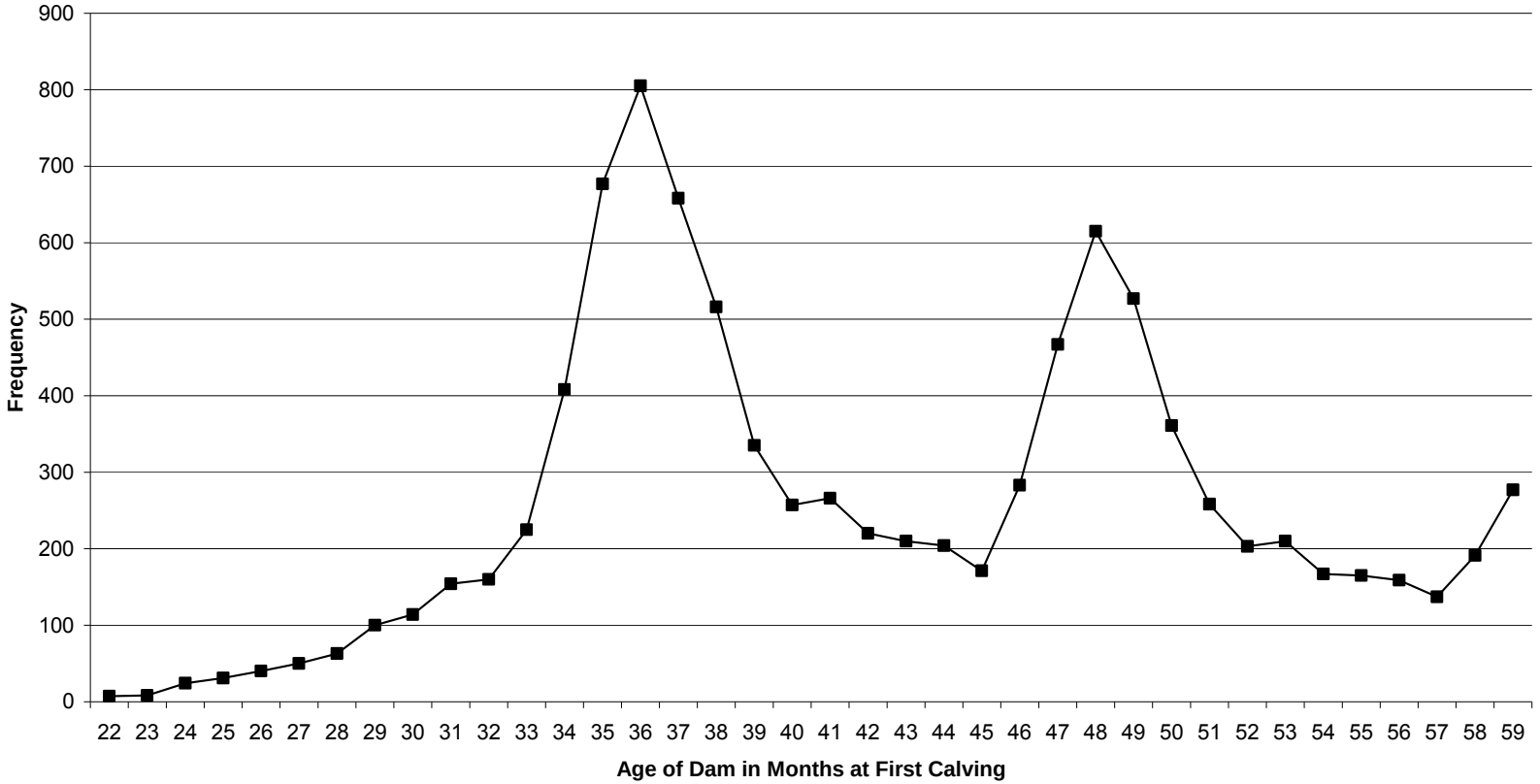

Figure 3.1 Distribution of age at first calving for Afrikaner beef cattle (months).

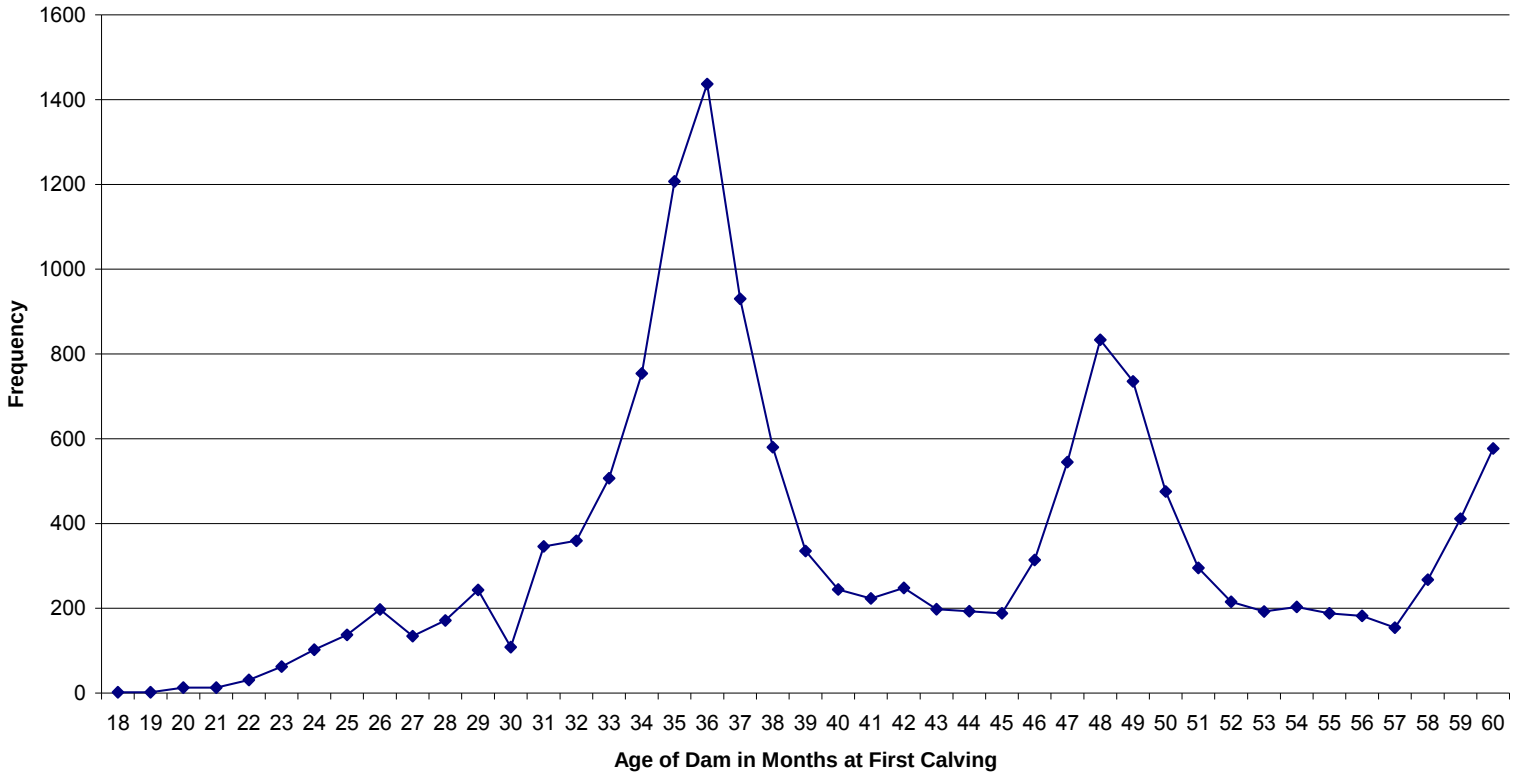

Figure 3.2 Distribution of age at first calving for Drakensberger beef cattle (months).

To investigate the structure of the data for the trait, a group of bulls were selected from each of the Afrikaner and Drakensberger breeds. Selected bulls had more than 20 daughters with measurements in at least 20 herds. These subsets of the original data sets (progeny of the selected bulls) were then used to predict estimated breeding values (EBVs) for age at first calving. The residuals from the GLM procedure of SAS were investigated within each sire for symmetry and skewness. These residuals were the sum of the genetic additive and error effects. The linear animal model was as follows,

$$Y = X\beta + Za + e$$

with y = vector of observations,

X, Z = known incidence matrices,

β = vector of fixed effects (herd x year x season effects)

a = vector of additive genetic animal effects and

e = vector of residuals.

With the assumptions $a \mid A, \sigma^2_a \sim N(0, A\,\sigma^2_a)$

$e \mid \sigma^2_e \sim N(0, I\,\sigma^2_e)$

$Cov(a, e) = 0$

From the assumptions of the linear animal model the residuals must be normally distributed, this is

$$Za + e \sim N(0, A_a\sigma_a^2 + I_e\sigma_e^2)$$

which implies a symmetric distribution of the data.

For age at first calving, the variance components were estimated with the REML VCE 3.2 software package (Groeneveld, 1994a,b) using the super-linearly converging quasi Newton optimising procedure, which approximates first derivatives on the basis of finite differences. EBVs and predicted error variances (PEVs) were estimated using Pest 3.2 (Groeneveld, 1990) that utilises the SMP solver from the Yale sparse matrix package. Full pedigree information for both breeds was used.

Data from Bonsmara beef cattle were used to investigate the trait days to calving. With the assistance of the Bonsmara Society, 10 herds were identified that regularly submitted mating lists over a period of 10 years. This data were then entered on INTERGIS by staff of SA Studbook Assosiation. The data consisted of 27 587 mating records of which only 22 281 bulls and dams could be linked to the National database of the NBCIS via registration numbers. There were, unfortunately, many obvious deficiencies in the data supplied. Of the total data collected 4 016 matings occurred during the 2000 and 2001 mating season of which offspring had not yet been born at the time of the study. A total of 17 762 calves were recorded from the rest of the matings. Of these, 4 169 calves appeared to be born before the joining date and 1306 were born between 0 and 260 days after the joining date. Since a cow's pregnancy duration is more or less 280 days, this was either impossible or questionable. Six hundred and eighty-three births occurred between 450 and 560 days after joining. It is reasonable to assume that these recordings were incorrect. All abovementioned data (inconsistent data) was omitted from the study. This left 7829 repeated calving records of 2980 Bonsmara cows. The pedigree information for the 2980 Bonsmara cows totalled 7829 animals. The general statistics of the Bonsmara data are presented in Table 3.3.

Table 3.3 General statistics of the data used in the days to calving investigation

	N	Min	Max	Avg	SD
		Age (months)			
Bonsmara	7 829	250	450	320	30

A further problem encountered was that submitted data did not always indicate whether a calf was born due to natural mating or artificial insemination (AI) and it was in some instances very difficult to disentangle one from the other.

The GLM procedure of SAS (1996) was used to determine the operational models that best describes the data. The final statistical model included the herd x year x season concatenation as a fixed effect. For days to calving, an animal repeatability model was fitted using the REML VCE4.2 software package (Groeneveld, 1994a,b; Groeneveld & García-Cortés, 1998), utilizing analytical

gradients (Neumaier & Groeneveld, 1998). The number of levels for each effect is presented in Table 3.4.

Table 3.4 Number of levels for fixed and random effects included in the final genetic analysis for days to calving for the Bonsmara breed

Factor	Type	Number of levels
Herd x year x season	F	447
Animal	A	7 829

F = Fixed

A = Random

Results

From Figures 3.1 and 3.2 it is clear that 60 was not an ideal cut off age for dams producing their first calf and it should rather have been 57 months for both the Afrikaner and Drakensberger breeds. It is also interesting to note that the first peak occurred around the age of 36 months for both breeds and the second peak 12 months later at 48 months of age, clearly indicating fixed seasonal breeding patterns employed by the breeders for both breeds.

It would be expected that a continuous trait such as the age at first calving of an animal will be a normally distributed trait. It is expected that if the average heifer of a breed is able to calve for the first time at the age of 36 months, all heifers should be able to achieve this. However, in South Africa breeders farm beef cattle in varying environments while utilizing different resources. This enables some breeders from favourable environments and resources to allow their heifers to breed earlier than would be possible for breeders farming in either harsher environmental climates or breeders utilizing challenging resources. Accepting that environmental constraints prohibit some breeders to breed heifers for first calving on average at 36 months of age, it is then reasonable to expect that the distribution within every herd*year*season concatenation should be normally distributed as demonstrated in Figure 3.3. From the graph it is clear that these distributions are not normal and have cut-offs to the right hand sides. The measure of skewness for the within

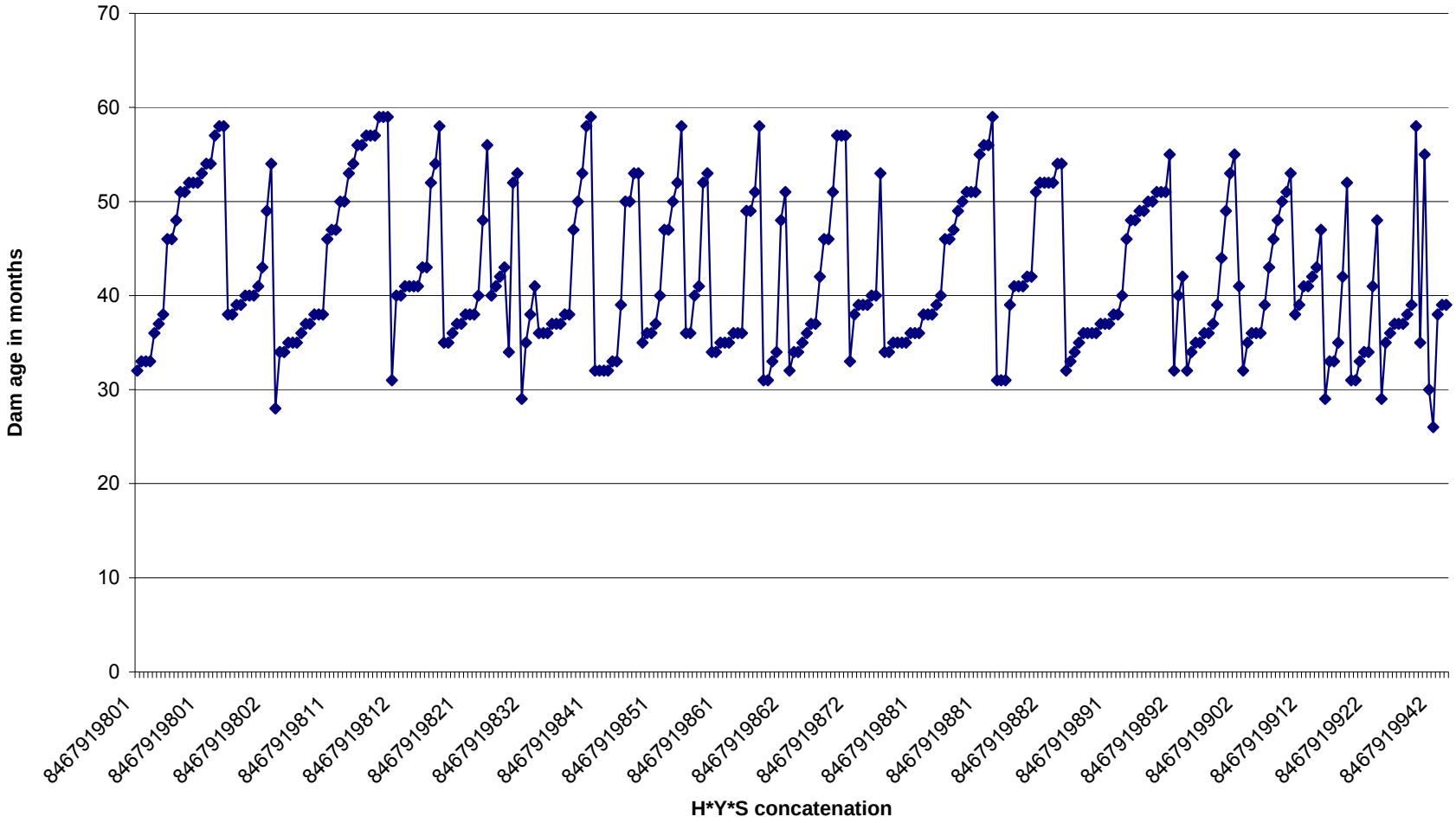

Figure 3.3 Example of age at first calving distribution within herd*year*season concatenation for herd 84679.

herd*year*season distributions range between 2.03 and 0.44 and the kurtosis of these distributions vary between -1.64 and 2.03.

After plotting the residuals (within sires), (Figure 3.4 and Figure 3.5 for the Afrikaner and Drakensberger, respectively), it is clear that the trait age at first calving does not comply with the normal assumptions of linear analysis.

The estimated variances and variance ratios for age at first calving are presented in Table 3.5. Optimization was done in two dimensions.

Table 3.5 Estimated variances and ratios for age at first calving

	Variances				Ratios	
	σ^2_a	SE	σ^2_e	SE	h^2	SE
Afrikaner	12.16	0.79	32.70	0.67	0.27	0.02
Drakensberger	21.28	1.21	49.87	1.06	0.30	0.02

σ^2_a = additive variance σ^2_e = error variance

The variance component estimation procedure for days to calving used 15 iterations and optimized with status one. The mean days to calving were 320±30 days. The minimum and maximum values were the cut-off values that were previously decided on the grounds of likely biological possibility described in the material and methods.

Using the VCE4.2 software, a heritability of 0.09 was estimated. This corresponds with the literature cited.

Discussion and Conclusions

When a heifer reaches puberty, numerous complicated mechanisms must coincide to show her first signs of oestrous. Hormonal activity from the pituitary gland and subsequently from the gonads is responsible for the occurrence of the first and following oestrous cycles throughout her life. Via these organs, the whole process is influenced by several factors of both hereditary and environmental nature. After oestrous, a cow must be able to become pregnant and sustain the pregnancy and then give birth to a calf before a measurement can be recorded for age at first calving and days to calving.

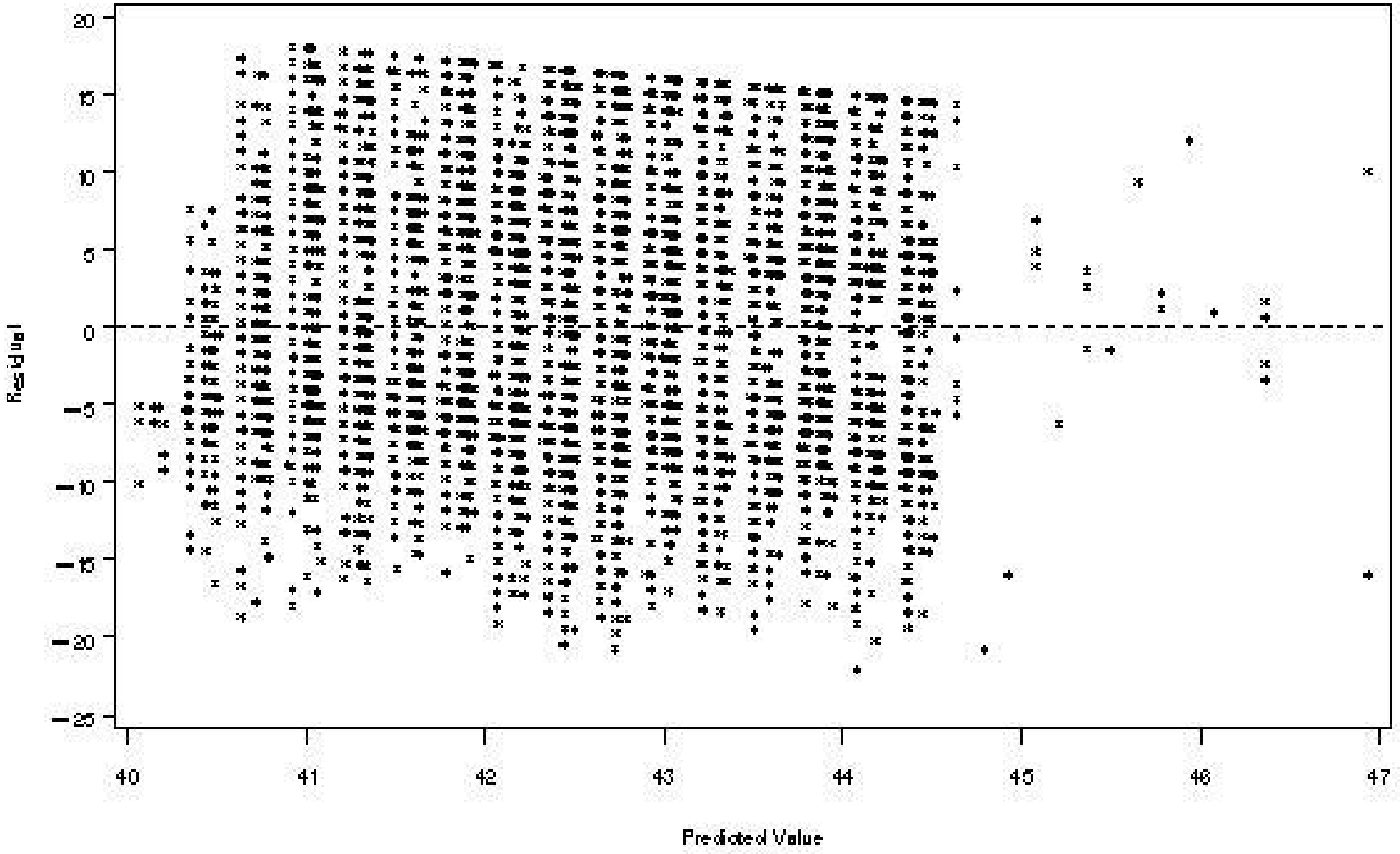

Figure 3.4 A residual distribution for age at first calving for Afrikaner cattle.

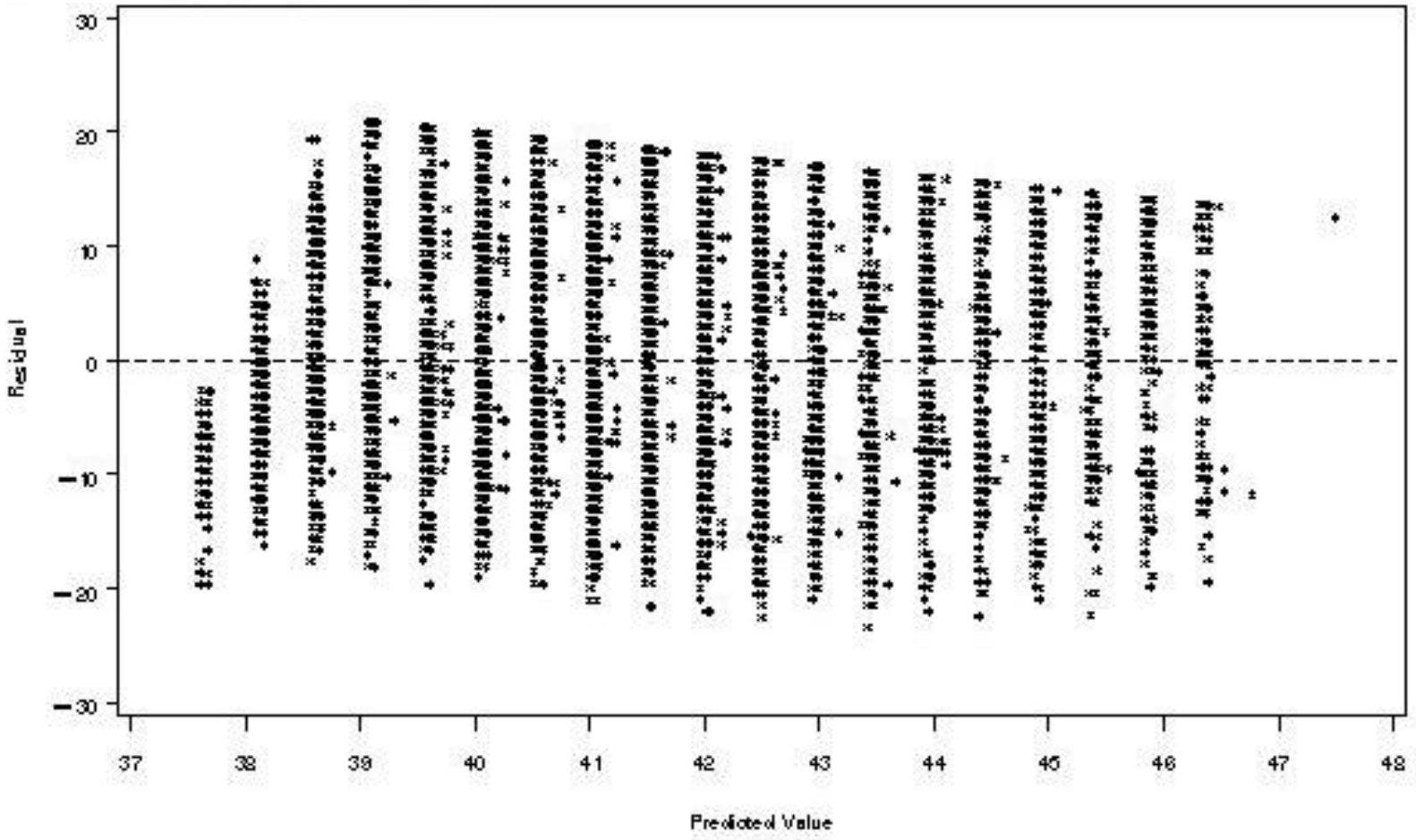

Figure 3.5 A residual distribution for age at first calving for Drakensberger cattle.

In most breeding systems, it is the decision of the breeder as to when and how long to mate heifers. Some breeders will breed their heifers earlier and so promote sexual precocity, whereas other breeders are restricted on when and how to breed heifers by resource and environmental constrains.

From Table 2.1 it can be seen that heritability estimates in the literature for age at fist calving varies between 0.03 and 0.44 with a mode of 0.09. The heritability estimated from data of heifers mated at ±12 months of age was high at 0.40 (Table 2.1) and can possibly indicate that age at first calving is more heritable when measured at younger ages. Age at first calving of both the Afrikaner and Drakensberger breeds were moderately heritable. This agrees with heritability estimates of 0.26 derived by Shanks *et al*. (1982) for age at first calving in first lactation dairy cattle, an estimate of 0.22 estimated by Oyama *et al*. (2002) on Japanese Black cows, an estimate of 0.44 estimated by Demeke *et al*. (2004) on Friesian, Boran and Jersey crosses and estimates of 0.22 and 0.26 estimated by Roughsedge *et al*. (2005) on Aberdeen Angus and Limousin, respectively. However, Grosshans *et al*. (1997) estimated a lower heritability (0.13) for New Zealand dairy cows in pasture bred seasonal production systems. Lower heritabilities were also estimated by Meyer *et al*. (1990), Peirera *et al*. (2002), Dias *et al*. (2004) and Roughsedge *et al*. (2005). Demeke *et al*. (2004) concluded that differences between breeds and individual cow variation were evident for age at first calving.

The genetic correlation between Holstein cows from Brazil and Columbia for age at first calving amounted to 0.78 (Cerón-Muñoz *et al.,* 2004). These authors concluded that a genotype x environmental interaction existed, as reflected by differences in ranking of sires between the two countries. A genotype x environmental interaction was not investigated in the present study, but it should be examined before EBVs is distributed to breeders for selection purposes.

Silva *et al*. (2005) estimated a correlation of -0.32 between age at first calving and heifer pregnancy rate, where heifer pregnancy was defined as a binary trait indicating the probability that heifers will become pregnant after exposure to the bulls. They concluded that age at first calving and the probability of heifers to become pregnant is determined by different genes. Selection for age at first calving will thus

not always indicate sexual precocity. They also propose that all heifers should be exposed to mating at a very young age when selecting for sexual precocity.

In this study, heritability estimates for age at first calving for both the Afrikaner and Drakensberger breeds were moderate and genetic progress might be achieved through selection for this trait. From literature cited, it seems possible that selection for animals that record a first calving earlier show greater sexual precocity.

As with age at first calving, the expression of genetic differences for days to calving is probably influenced by management strategies in individual herds. Although the additive variance estimated for days to calving agrees with the literature (Table 2.1), the inadequacies of the original data provided for the investigation are multiple. After editing only one third of the original records obtained was used in the genetic analysis. This emphasizes the large margin of error when data is recorded on farm without a validation system. This result supports a motivation why a national database, with a process of data validation, is crucial. Furthermore, data for days to calving must be recorded by all herds participating. One of the reasons why the data are so inadequate is possibly that no feedback was given to breeders on their mating list recordings. If some form of feedback were given, breeders would probably have recorded them with greater care. In future, feedback must be given to encourage the accuracy of mating list recordings on farm. However, the results from the edited records suggest that heritability estimates accorded well with literature estimates, thereby suggesting a measure of robustness.

Since the AI and natural mating data are so confounded in the herds where AI is used, it is recommended that only herds that do not use AI should record days to calving, unless the AI and natural mating data can be indicated very clearly. The general practice in South Africa among Bonsmara beef herds where both AI and natural mating are practised is to inseminate the cows two weeks prior to joining them to the bull. In this way any cow not conceiving from AI will be impregnated by the bull without unduly lengthening her inter-calving period. This is a very practical and workable management policy to follow in a beef cattle herd and breeders will not be inclined to extend the period between AI and joining to much longer than two weeks. As a result it allows for a very short period of possible confusion as to

whether, due to varying gestation lengths, a specific cow conceived from AI or from natural mating.

A major obstacle when analysing age at first calving and days to calving is the inadequate structure of the data. For age at first calving it can probably be attributed to at least three factors. Firstly, the age of the cow at first calving is dependent on the timing as well as the duration of the mating season employed by the breeder. Secondly, by restricting the exposure of heifers to a bull by using a strict breeding season policy, creates a cut off to the right hand side of every within herd*year*season concatenation distribution. Finally, due to various managerial reasons, some cows did in fact calve earlier but the fist calf was never recorded on the NBCIS. Significant skewness clearly indicates that data is not normally distributed. If a data set exhibits significant skewness, one approach is to apply some type of transformation to try to make the data normal. Another approach is to use techniques based on distributions other than normal. For example, the exponential, Weibull, and lognormal distributions are typically used as a basis for transforming data rather than assuming normality (Life data (Weibull) analysis reference, www.weibull.com).

For days to calving, however, problems in the structure of the data arise when penalties are imposed on open cows. Penalties for cows not calving in a specific season were introduced by Johnston & Bunter (1996). They proposed adding 21 days penalty to cows not calving in a breeding season. These 21 days were added from the last possible calving date of any cow in the same herd with similar a joining date. By doing this a point 21 days on the right of the normal distribution is created where numerous observations are recorded. Thus, the number of cows that failed to calve will distort the possibility of a normal distribution.

Both age at first calving, as well as days to calving are component traits that are easy and cheap to measure. Being component traits, they are traits that are measured at fixed events in the life of a cow. A further advantage is that both traits can be measured at all levels of management intensity. As estimated by numerous authors, both traits have favourable genetic correlations to sexual precocity and other lifetime production traits. Addressing the problems highlighted in this chapter concerning both recording and evaluating age at first calving and days to calving and

finding solutions for the obstacles, will enhance the probability to genetically improve the fertility of female animals in a herd or in the national population. It is proposed that a different approach to penalizing open cows is implemented before the trait days to calving would be suitable as an indicator trait of female fertility in a national evaluating system.

With respect to both age at first calving and days to calving, there is a need for guidelines to standardise the recording practice in order to obtain meaningful information on female reproductive performance. Suggestions as to what these guidelines should include are:

1. Recording of all joining dates and
2. recording of contemporary groups when cows are joined to the bulls.

When these guidelines have been formalised, the recorded information can be utilized to estimate genetic variance components as well as BLUP breeding values that can be used to improve the selection efficiency for fertility in the national beef population. Selecting data for the estimation of variance components and EBVs for age at first calving and days to calving both needs a different approach. The selection would appear to be biased when selecting cows based on the records currently available.

Chapter 4

Aggregate traits: Calving Rate and Calving Success

Introduction

From Chapter 2 the difficulties in defining female reproductive merit are clear. Very often no records exist of reproductive ability except those that can be deduced from birth dates. This makes it difficult to identify economically important traits relating to reproduction that can be used in routine evaluations. In Chapter 3 two component traits, age at first calving and days to calving, were investigated. Opposed to component traits, aggregate traits are composites of more than one event in the lifetime of a cow (Figure 1.1). To measure aggregate traits, more than one event must occur and be measured in the lifetime of a cow. This can potentially increase the influence that effects, both environmental and genetic, can have on the expression of aggregate traits. In this chapter, two aggregate traits, identified in Chapter 2 as traits that show merit for inclusion in a national recording system, will be investigated as possible indicators of genetic female reproduction efficiency of beef cattle.

Calving rate is a lifetime measure of the reproductive performance of a cow. It is defined as the number of calves born divided by the number of opportunities a cow has had to produce a calf. If opportunities are defined as the number of years in which the cow could have produced a calf, calving rate comes close to the overall breeding objective as defined in Chapter 1 and, therefore, seems to be a useful trait when aiming to improve the female reproductive performance of a herd. For cows with only one parity, calving rate is a binary trait while it becomes more continuous as the number of parities increases.

Martinez *et al.* (2004) investigated genetic parameters for six measures of length of productive life and three measures of lifetime production by six years after calving for Hereford cows. Length of productive life given the opportunity was measured as days between first calving and culling. Heritability estimates for the

length of reproductive life was low to moderate and ranged from 0.05 to 0.15. Length of productive life has similarities with calving rate as it was defined in this study. Both traits take the entire productive life (i.e. production of calves) into account.

Calving success can be defined for each cow in the herd for each year. Calving success is, therefore, a binary trait with either ones for successful calvings or zeros when no calf was born. Although very similar to calving rate, this trait has multiple measurements (a measurement with each parity) for each cow and is evaluated as a repeatable trait in genetic analysis.

In a threshold-linear two trait analysis a strong favourable correlation between calving success and days to calving was estimated by Donoghue *et al*. (2004a,b), indicating that selection for a reduction in days to calving will result in improved calving success.

The aim of the study is to evaluate the merit of the aggregate traits, calving rate and calving success as indicators of female reproductive efficiency.

Materials and Methods

Field data were obtained from the Integrated Registration and Genetic Information System (INTERGIS) of South Africa for pure-bred Afrikaner, Drakensberger, SA Angus and Simmentaler beef cattle for the period 1976 to 1998. The data were edited to eliminate animals with unknown birth dates. Dams born before 1973 were eliminated from the data since the integrity of the earlier data could not be verified. All the calves of embryo donor cows were omitted as well as all animals of contemporary groups with less than 10 animals.

The first trait to be investigated was calving rate, a lifetime reproduction trait similar to calving rate defined by Meyer *et al.* (1990). Given the limited information available, calving rate was defined as the number of calves born to a cow divided by the cow's age. The minimum observation was 0.08 and the maximum value 1.00 with an average of 0.44 and standard deviation 0.15. These values were then multiplied by 100 so that the observations were between 0 and 100. The herd entry and exit date information of individual cows are not recorded in the South African recording schemes. The entry date of each cow was thus replaced by birth date, while its exit date was replaced by the cow's last available calving date.

A second trait, calving success, was defined as a binary trait. Breeders in Southern Africa breed their heifers at varying ages depending on breed type and resources available. Breeders, especially those of some of the indigenous breeds (Zebu and Sanga breeds), do not breed heifers to calve before on age 3 years. Eler *et al.* (2004) also concluded that for populations of *Bos taurus* origin, most animals reached puberty at yearling age as compared to Nelore cattle (*Bos indicus*) that only reached puberty at later ages. Therefore, two approaches were used arbitrarily to define the parameters of the observations for the different breeds used in this investigation of calving success. These approaches were:

1. For the two indigenous breeds (Afrikaner and Drakensberger) it was expected of all heifers to calve for the first time at the age of three years. If she failed to do so, a calving success of zero was assigned in her third year. For a successful calving before the age of three years, the score for calving success is 1.
2. For the European breeds (SA Angus and Simmentaler) it was expected of all heifers to have calved for the first time at the age of two years. If she failed to do so, a calving success of zero was assigned in her second year. For a successful calving before the age of two years, the score for calving success is 1.

Any cow calving before her first expected calving date was credited for this performance and her record commenced at the year of first calving and a calving success score of 1 was allocated to such heifers.

Full pedigree information of all the breeds was used in their respective analyses. All pedigrees were also checked to ensure all parents were born at appropriate times before their offspring. Characteristics of the data structure with the phenotypic means and standard deviations are summarized in Table 4.1.

To test whether results obtained from the complete data sets for calving rate and calving success were not a symptom of the data structure, a selected data set on the Afrikaner was constructed from proven sires.

Requirements for this selected data set were:

1. all sires selected were used in more than four herds
2. all sires had to sire more than 75 offspring
3. at each herd*year level the measurements of more than 9 dams were available.

This resulted in a selected data set of 3922 measurements. The general statistics of the selected Afrikaner data are given in Table 4.1.

The REML VCE4 package (Groeneveld, 1994a,b; Groeneveld *et al.*, 1996; Groeneveld & García-Cortés, 1998) was used to estimate the variance components utilizing analytical gradients (Neumaier & Groeneveld, 1998) for both traits. For variance component estimation of calving success, a repeatability model was used.

Two models were fitted for both traits to investigate whether herd*year interactions should be fitted as fixed or random. For calving rate, two herd-year effects were included in the model, the first being the herd and year the dam was born in (DHerd*year) and the second the herd and year of her last calf (CHerd*year). For calving success, the age of the dam in years was included as a fixed effect in all the models. In matrix notation the model for both traits and all breeds are:

$$y = X\beta + Zu + e ,$$

where: y = vector of observations

X, Z = incidence matrices for all fixed and genetic effects, respectively

β, u = vector of unknown parameters for fixed and animal effects, respectively

e = vector of residuals

With the assumptions $u \mid A, \sigma^2_u \sim N(0, A\,\sigma^2_u)$

$e \mid \sigma^2_e \sim N(0, I\,\sigma^2_e)$

$Cov\,(u, é) = 0$

On the selected data set of the Afrikaner sires, for calving success only, a sire model was performed to substantiate the results from the animal model analysis:

$$y = X\beta + Zu + e ,$$

where: y = vector of observations

X, Z = incidence matrices for all fixed and genetic effects, respectively

β, u = vector of unknown parameters for fixed and sire effects, respectively

e = vector of residuals

With the assumptions $u \mid A, \sigma^2_u \sim N(0, A \sigma^2_u)$

$e \mid \sigma^2_e \sim N(0, I \sigma^2_e)$

$Cov (u, é) = 0$

To determine the heritability for calving success on the underlying scale, a GFCAT (Konstantinov, 1992) sire model analysis was performed on the selected Afrikaner data set. The location parameters (η) were modeled as:

$$\eta = X\beta + Zu$$

where: X, Z = incidence matrix for all fixed and genetic effects, respectively

β, u = vector of unknown parameters for fixed and sire effects, respectively.

With the distribution of random effects:

$u \mid A, \sigma^2_u \sim N(0, A \sigma^2_u)$

Table 4.1 General statistics of the data

Trait	Breed	Number of records	Number of animals in pedigree	Average	SD
CR	Afrikaner	340 566	46 570	0.441	0.153
	Afrikaner – Selected data	927	2 803	0.551	0.150
CS	Afrikaner	209 420	50 028	0.608	0.488
	Afrikaner – Selected data	3 922	192	0.744	0.418
	Drakensberger	132 165	31 164	0.699	0.459
	SA Angus	89 752	21 680	0.716	0.451
	Simmentaler	250 000	62 197	0.751	0.432

CR – calving rate

CS – calving success

SD – standard deviation

Results

The final model for calving rate is presented in Table 4.2, resulting in around 53 141 Mixed Model Equations for the complete Afrikaner data set and 2 998 equations for the selected Afrikaner data set.

The estimates and corresponding derived ratios for calving rate are presented in Table 4.3 for the models including the Dherd*year and Cherd*year effects as fixed or random. The analysis for calving rate on the selected Afrikaner data using the linear animal model, resulted in similar results to those from the complete Afrikaner data set.

For calving success, the final models for all four breeds are given in Table 4.2 resulting in 55 000, 34 000, 24 000 and 69 000 Mixed Model Equations for the Afrikaner, Drakensberger, SA Angus and Simmentaler, respectively. The estimates and corresponding derived ratios for calving success are presented in Table 4.4 for the models including the herd-year effect as fixed or random. The status at the end of the optimization is given. When optimization did not finish with status 1, no standard errors are given, since convergence could not be achieved.

Table 4.2 The final statistical models used for calving rate (CR) and calving success (CS)

Y	Model	Factor	Type	Number of levels			
				Afrikaner	Dr'berger	SA Angus	Simmentaler
CR	AM	Dherd*year	F/R	3 088			
		Cherd*year	F/R	3 483			
		Animal	A	46 570			
	AM	Dherd*year	F/R	86			
	Selected	Cherd*year	F/R	109			
	data set	Animal	A	2 803			
CS	AM	Herd*year	F/R	4 960	2 479	1 930	6 328
		Dam age	F	19	19	19	21
		Animal	A	50 028	31 164	21 680	62 197
	SM	Herd*year	F/R	261			
	Selected	Dam age	F				
	data set	Sire	S	192			

AM - Animal Model
SM - Sire Model
F - Fixed
R - Random
A – Animal
S - Sire
Dherd x year- herd and year the dam was born in
Cherd x year – herd and year the calf was born in

Table 4.3 Variances and ratios (expressed as proportion of total phenotypic variance) for calving rate from Afrikaner beef cattle

Mo-del	Data	Fixed/ Random	Variances				Ratios				Status	Standard errors			
			σ^2_e	σ^2_a	σ^2_{Dhy}	σ^2_{Chy}	e	h^2	Dhy	Chy		e	a	Dhy	Chy
AM	Total	F	0.01	0.00			0.96	0.04			1	0.01	0.00		
	data set	R	0.01	0.00	0.01	0.01	0.31	0.03	0.29	0.37	1	0.00	0.00	0.00	0.00
	Selected	F	0.01	0.00			0.94	0.06			1	0.07	0.07		
	data set	R	0.01	0.00	0.01	0.01	0.36	0.02	0.26	0.36	1	0.03	0.03	0.03	0.03

AM – Animal Model
F - Fixed
R - Random
Dhy - herd and year concatenation the dam was born in
Chy– herd and year concatenation the calf was born in

Table 4.4 Variances and corresponding ratios for calving success with herd-year included as a fixed and random effect in the model. The status at optimization is indicated

Mo-del	Breed	Fixed/ Random	Variances			Ratios			Sta-tus	Standard errors		
			σ^2_e	σ^2_a	σ^2_{hy}	e	h^2	hy		e	a	hy
AM	Afrikaner	F	0.17	0.00		1.00	0.00		2			
	Drankensberger		0.13	0.00		0.99	0.02		1	0.00	0.00	
	SA Angus		0.13	0.00		1.00	0.00		1	0.00	0.00	
	Simmentaler		0.14	0.00		1.00	0.00		1	0.00	0.00	
SM	Afrikaner	F	0.14	0.00		1.00	0.00		1	0.00	0.00	
AM	Afrikaner	R	0.17	0.00	0.08	0.67	0.00	0.33	2			
	Drankensberger		0.13	0.00	0.10	0.57	0.01	0.43	1	0.01	0.00	0.01
	SA Angus		0.13	0.00	0.04	0.75	0.00	0.25	1	0.01	0.00	0.01
	Simmentaler		0.14	0.00	0.05	0.74	0.00	0.26	1	0.00	0.00	0.00
SM	Afrikaner	R	0.14	0.00	0.05	0.76	0.00	0.24	1	0.02	0.00	0.02

AM – Animal Model
SM – Sire Model
F - Fixed
R - Random
hy - herd-year concatenation

The analysis for calving success on the selected Afrikaner data using the linear sire model resulted in similar results to those from the complete Afrikaner data set using the linear animal model. Results from the linear sire model analysis of calving success are presented in Table 4.4.

Using the GFCAT sire model for analyzing the selected Afrikaner data set, proved that genetic variation does exist for calving success on the underlying scale. The σ^2_e / σ^2_s ratio was estimated as equal to 13.736 with the corresponding σ^2_s = 0.0728 and h^2 = 0.27 indicating a moderate to high heritability on the underlying scale.

Discussion

When consideration is given to aggregate traits as indicators of female reproductive ability in beef cattle, a vast number of influences and effects, both genetic and environmental, will influence the performance of a female animal. Since aggregate traits are measured over more than one event in the lifetime of a cow, a cow that performs well in an aggregate trait will have to perform well in more than one event simultaneously or events measured over a period of time. Numerous influences on many stages over the measurement period of the trait, can thus impact eventually on the measured performance for a cow.

While calving rate comes close to the overall breeding objective, overall reproductive efficiency (ORE), it does have serious deficiencies. The first problem lies in the lack of information about the individual cow's herd entry and exit dates. As a substitute, the entry date was replaced by the birth date of the cow while its exit data was replaced by the cow's last available calving date. The effect of this was to exclude variation (also genetic variation if it exists) from this trait, because all animals ended their reproductive life with a calving. Cows which did not conceive or did not produce another calf, although it stayed in the herd for perhaps another year, got the same trait measurements as a cow that got culled right after calving. Thus, calving rate, as defined in this study, captured a reduced amount of total variation in reproductive performance. How this affected the derived heritability estimates is not clear. It could be argued that much of the culling is due to reproductive failure.

Omission of information that possibly contribute to an additive genetic component resulted in an underestimate of the true additive heritability.

Replacing the true entry date of a cow into the herd with its birth date possibly had a similar effect as it increased the overall variation, including differences in managerial policies, resulting in genetic components estimated on the basis of calving rate as defined, to be an underestimate.

Being a lifetime statistic, calving rate is made up from a different number of calvings. It depends on the parity of the cows with the result that the accuracy of calving rate varies with the number of different parities. To model this effect correctly, different residual variances should be used depending on the number of calves included in each calving rate. While this could be done rather easily for the components of the BLUPs, it was not possible to include this into REML variance component estimation on the basis of analytical gradients, which was the procedure followed.

Another problem related to a lifetime statistic is the inability to adjust for environmental effects in a proper way. A cow with eight calves may have produced these over years with possibly very different environmental conditions. As the cow's calving rate is based on all eight calvings it is not possible to adjust for each individual calving. The effect of this will be an inflation of the residual variance, which in turn will lower the heritability.

In conclusion, calving rate as defined here does have severe limitations and most probably underestimated the true additive genetic variation for a properly defined calving rate. Thus, the estimates obtained should be considered as the lower bounds of the true estimates. From the literature (Table 2.1) heritabilities range for calving rate between 0.02 and 0.17 when including open cows.

To try and overcome some of the difficulties experienced with calving rate, a trait named calving success was defined and investigated. However, some serious constraints exist for this trait as well, as no information was available for cows that did not calve. Zero values were thus allocated if no calf was recorded during a year. Non-calving migrates were allocated to the next herd.

Differentiating between indigenous and European breeds, allowing the indigenous breeds to record first calving only at the age of three years, must rather

be done on a less arbitrary basis and every herd must rather be investigated to determine a specific breeding trend. Age classification should thus rather in future be on within herd basis and not for a breed type in general as was done in this study.

The problems caused by not knowing the exit date of a cow have already been outlined. For calving success, the last record available for each cow is always success, which clearly does not reflect reality. Thus, the true calving success estimate will be lower.

The way calving success is defined, repeated records for each cow is available. Compared to calving rate, the accuracy will increase, as different numbers of calves per cow will automatically considered in the repeatability model. Furthermore, each calving can now be adjusted to the relevant environmental effects. Thus, calving success will have better properties than calving rate. However, calving success is a binary trait, which violates BLUP model assumptions, assuming normality.

From the analysis done on all four breeds, it seems that no additive genetic variation exists for calving success. It could be concluded that no additive genetic variance exists for calving success in Southern African beef breeds, but investigation must be done into other possible reasons for these results.

Firstly, it could be that the non-genetic effects (herd-year interactions of the dam and herd-year interactions of the calf) included in the model, did not describe the data adequately and resulted in an inability of linear mixed models to properly partition the genetic components. Whether these non-genetic effects were fitted as fixed or random, did not influence the results obtained in this study (Tables 4.3 and 4.4). Secondly, some discussion is needed on the methodology used to analyze the data. In the study done by Meijering & Gianola (1985a), ranking properties of linear (BLUP) and non-linear (GFCAT) methods of sire evaluation for dichotomous or ordered categorical responses were compared. The endpoint measured was the Monte Carlo realized response to truncation selection upon predicted sire values. They concluded that, when a mixed model was required to describe variation of binary responses, GFCAT performed significantly better than BLUP when heritability in the conceptual underlying scale was moderate to high. Contrary to this, Matos *et al.* (1997) concludes that the goodness of fit of linear and non-linear models was

similar, and with respect to prediction ability, differences between linear and non-linear mixed models were negligible.

Unfortunately no variation was detected for calving success using REML models, however, using a GFCAT sire model on the selected Afrikaner data set, a heritability of 27% was derived. This result seems to indicating that genetic variance for calving success exist on the underlying scale.

Conclusions

At this point in time neither of the two traits investigated, namely calving rate and calving success, seems to be options for expressing the reproductive merit of animals in a Southern African analysis using mixed model methodology. The heritability of calving rate is low (0.04), resulting in slow potential genetic improvement. Furthermore, at the time of this study, there were no methodologies available at present to accommodate data where the residual variance of each observation differs.

Because the data were not recorded for the purpose of describing reproduction performance, there are too many problems and assumptions made when analyzing calving success. From this study, it must be concluded that REML is not the correct methodology to estimate variance components for a binary trait such as calving success.

In the light of the above, it seems reasonable to make the following recommendations to the South African recording schemes:

1. All entry and exit dates of heifers and cows should be recorded.
2. The pregnancy status of the animals should be known when entering or exiting a herd.
3. All joining dates should be recorded, and if no calf results from a joining, this fact must also be recorded.

Chapter 5

Non-linear model analysis of categorical traits related to female reproduction efficiency

Introduction

Female reproductive potential is often defined in the literature as a threshold trait because of the categorical nature of the observation, i.e. the cow either calved or she did not. Threshold models assume the existence of an underlying, unobservable normal distributions that is categorized through fixed thresholds. For example, when a trait is phenotypically expressed in only defined forms, even though diverse combinations of genetic as well as environmental influences determine the phenotype, such a trait is called a threshold trait. The phenotypes that are observed, depends on the underlying tendency to develop in one form rather than the other, depending on where it is situated relative to the threshold (Wright, 1920, 1926; Bliss, 1935; Dempster & Lerner, 1950).

Threshold traits are governed by multiple genotypes, expressing themselves in two or more phenotypic categories. The genotypes vary according to their closeness to the threshold. The first category individuals may differ widely in whether they are near the threshold or far below it. Likewise, some will almost reach the threshold and are genetically close to those just above it. Even a large change in an individual's genotype will have no observable phenotypic effect unless that change moves the specific individual across the threshold. If it does, even a small change in the genotype will have a large phenotypic effect. A trait may have more than one threshold. If the individuals with the undesired phenotype are numerous, discarding them may exhaust most of the breeder's freedom to cull. If the population can survive biologically for a few generations and if the breeder can survive financially, mass selection is likely to make the frequency of the undesirable phenotype less although it is not likely to make it disappear altogether (Lush, 1994).

Exposure to harsh environmental conditions such as drought, extreme heat or cold, and low levels of nutrition, will show the breeder which individuals and families have is the most tolerant the adverse conditions. Falconer (1989) refers to this as “genetic assimilation” and refers to earlier work described by Waddington (1953). Year-to-year fluctuations in the threshold, because of changes in the general environment, will inevitably cause year-to-year fluctuations in the expression of fertility.

The basic theory of threshold models has been given by Gianola & Foulley (1983), Harville & Mee (1984), Gilmour *et al*. (1985) and Misztal *et al.* (1989). By adding an additional subroutine in the existing programs for linear models Misztal *et al.* (1989) were able to accommodate threshold models. The modified model used in this study was as follows:

$$\begin{bmatrix} \mathbf{X'W}^{[i-1]}\mathbf{X} & \mathbf{X'W}^{[i-1]}\mathbf{Z} \\ \mathbf{Z'W}^{[i-1]}\mathbf{X} & \mathbf{Z'W}^{[i-1]}\mathbf{Z}+\mathbf{G}^{-1} \end{bmatrix} \mathbf{x} \begin{bmatrix} \boldsymbol{\beta}^{[i-1]} \\ \boldsymbol{\mu}^{[i-1]} \end{bmatrix} = \begin{bmatrix} \mathbf{X'W}^{[i-1]}\tilde{\mathbf{y}}^{[i-1]} \\ \mathbf{Z'W}^{[i-1]}\tilde{\boldsymbol{\mu}}^{[i-1]} \end{bmatrix}$$

where:

X, Z = design matrices

W = diagonal matrix

β = vector associated with fixed effects (herd, year and season of birth of animal)

μ = vector of sires

G = variance-covariance matrix of sire effects

$G^{-1} = A^{-1}/\sigma^2_s$

where: A^{-1} = inverse of the relationship matrix

σ^2_s = sire variance

Reproductive traits often show uncertain binary responses for success or failure for the trait measured. Spangler *et al.* (2006) investigated two methods of analyzing the data. Firstly, a threshold model ignoring uncertainty, and secondly, a threshold model accounting for uncertainty via fuzzy logic classification. They concluded that a threshold model has advantages over alternative methods when the data is of binary nature to avoid bias when estimating genetic parameters.

Given the restrictions of the South African recording system in the past, as described in the Chapters 2, 3 and 4, an attempt was made to define new additional traits in order to utilize the recorded data, historically available, to its full potential. The aim of this study was to define some additional categorical traits related to female reproduction efficiency and to estimate the variance components for these traits using non-linear threshold (GFCAT) models and to investigate their possible inclusion in national genetic evaluations in South Africa.

Materials and Methods

Data from the National Beef Cattle Improvement Scheme (NBCIS) of the Afrikaner beef breed in South Africa for the period from 1976 to 2001 were used. The original selected data set consisted of 36 880 animals before editing. Animals born from embryo transfer were omitted from the data. Three traits, considered to describe aspects of female fertility potential and efficiency were defined.

The first trait, retention, identifies heifers that are retained in the herd as breeding cows. In beef cattle breeding, it is preferable that female animals stay in the herd as breeding cows for longer periods. Animals that rebreed after the first and second calving are often the animals that stay in the herd for longer, displaying good genetic merit as breeding animals. Breeders tend to cull animals that fail to rebreed after the first or second calving.

The second trait, stayability, is defined as an indicator of the staying ability of a cow in the herd once she is selected as a breeding heifer. The stayability of cows in a herd can vary from breed to breed and will determine the manner and intensity of selection for other fertility traits since it influences the age structure of the breed. Therefore, stayability is an important trait to include in a study regarding female

fertility of a breed. Animals that tend to stay in herds for many years display good adaptation with the consequence of breeding good adapted offspring.

The third trait, calf tempo, describes the rate at which a cow calved up to a specific age after being chosen as a breeding heifer in the herd. In beef cattle herds, it is not economically viable to keep cows that do not breed every year. Therefore, if breeders can select cows that tend to breed regularly, such an animal will have a greater economic value than an animal that skips a calving opportunity. Thus, being adapted to the environment and staying in the herd for many years alone, will only be economically beneficial if that cow gives birth to a calf every year she is given the opportunity to do so.

For the Afrikaner breed, heifers are rarely bred to calve before the age of three years. Rebreeding after first calving is often a challenge, and once a cow can overcome this hurdle, she will usually be retained as a breeding cow in the herd. Calf tempo will allow the breeder to make a distinction between cows that rebreed after the first calving and those that tend to delay before rebreeding. The three traits were defined as follows:

1. Retention: Heifers were considered that were present in the herd at the age of 18 months. If she proceeded to record the birth of a calf at any stage later in her lifetime, she was placed in category 1. If she failed, and the birth of a calf was never recorded for her, she was placed in category 0.
2. Stayability: If a cow calved at any stage for any number of times before she reached the age of 6 years, she was placed in category 0. If she calved again at any stage for any number of times after the age of six years, she was placed in category 1.
3. Calf tempo: Heifers were considered that were present in the herd at the age of 18 months and evaluated up to the age of 5 years. Thus, only females that were weighed at 18 months and then stayed in the herd to the age of at least 5 years or older, qualified for inclusion in the analysis. If she recorded the birth of a calf once before reaching the age of 5 years, she was placed in category 1, and if she recorded two or more calves before the age of 5 years, she was placed in category 2. If the heifer failed to record

the birth of a calf before she reached the age of 5 years, she was placed in category 0. Since the definition of the rate of calving in this study differ from that of Meyer *et al.* (1990) and Rust & Groeneveld (2002), it was decided to refer to this trait as calf tempo rather than calving rate to avoid confusion.

The cut-off ages of 18 months, 5 years and 6 years were chosen arbitrarily. It is assumed that heifers still present in the herd at the age of 18 months are kept as replacement heifers and will usually be mated at some future time, depending on the management system employed by the farmer. Heifers not suitable as replacement heifers, are usually culled before 18 months. For calf tempo it was reasoned that a breeding heifer should show her reproductive potential by the time she is 5 years old, overlapping the critical second calving period when many heifers often falter. For stayability, the aim is to determine the retention of cows in the herd. Since the Afrikaner cow is known to often breed up to an age of 16 – 20 years it was decided to extend the defining cut-off age for stayability in the Afrikaner breed to 6 years. Similarly, Silva *et al.* (2003a) defined stayability as whether a cow had calved in a herd at a specific age given that she had calved at an earlier age. The cut-off ages Silva *et al.* (2003a) studied were five, six and seven years.

The general statistics of the data for the three traits retention, stayability and calf tempo are presented in Table 5.1. Initially 7746 Afrikaner female records from 473 sires calving in 78 herds were used for the genetic parameter estimation using threshold models for retention. The corresponding numbers were 3018 Afrikaner females from 243 sires calving in 51 herds for stayability and 7653 Afrikaner females from 465 sires calving in 82 herds for calf tempo. All sires and herds were represented in both categories for retention and stayability and in at least two categories for calf tempo.

Table 5.1 Numbers of the edited data and general statistics for retention, stayability and calf tempo

	Retention	Stayability	Calf tempo
Animals	7 746	3 018	7 653
Sires	473	243	465
Herds	78	51	82
Year*seasons	32	31	35
Herd*Year*Season	655	469	706
Min observation	0	0	0
Max observation	1	1	2
Average	0.45	0.34	0.37
SD	0.50	0.47	0.62

Heritability on the underlying scale was estimated for all three traits as:

$$h^2 = \frac{4\sigma^2_s}{(\sigma^2_s + \sigma^2_e)}$$

The software used in these threshold analyses, GFCAT, was adapted by the University of the Free State, South Africa (Konstantinov, 1992). It is a set of Fortran programs calculating variance components and breeding values using threshold mixed models. A relationship matrix due to sire relationships was used to support the model. For the GFCAT procedure the herd*birth year*season concatenation was included in the model. The birth year for the cows ranged from 1976 up to 1990.

Results

The sire variances and derived heritability estimates on the underlying scale for retention, stayability and calf tempo are presented in Table 5.2. A large sire variance of 0.202 with a resulting heritability of 0.67 on the underlying scale was estimated for retention.

As for the stayability of a bull's female progeny, a sire variance of 0.072 with a heritability estimate on the underlying scale of 0.27, which was considerably lower, was obtained. For the rate at which a bull's female progeny calved before they reached the age of 5 years, a moderate to high sire variance of 0.114 (with heritability on the underlying scale of 0.41) was estimated.

Table 5.2 Summary of sire variances and heritability estimates on the underlying scale for retention, stayability and calf tempo using threshold models

Trait	Sire Variance	h^2 (underlying scale)
Retention	0.202	0.67
Stayability	0.072	0.27
Calf tempo	0.114	0.41

Discussion

Failure to reproduce is the most common cause for culling beef cows reared under extensive farming conditions. Thus, by assuming that other culling reasons are unimportant, the ability of a cow to be retained in the breeding herd may be considered as an indicator trait for female fertility.

The large sire variance estimated for retention, enables the beef breeder to effectively select bull progeny from those bulls of which the female progeny was more likely to be retained in the national herd as breeding heifers, as sires for the next generation. The heritability estimate of 0.67 on the underlying scale is large. Retention does, however, not only reflect the fertility of the female progeny of a bull, but may also reflect a preference of breeders for a specific bull and its female progeny. The fertility reflected by this trait is an indication of the fertility displayed by a bull's heifers, as it is often the practice in beef breeding to select heifers into the national herd that fall pregnant when mated in a short breeding season. The likeliness of the females will also be reflected by retention. So, using retention as a primary predictor of the fertility of a bull can be misleading in some instances, since some breeders give preferential treatment to those heifers from, for example, an expensive bull or females that display specific breed characteristics very well.

Stayability reflects the ability of a bull's female progeny to remain in the national herd as breeding cows for a few years after initially being selected as breeding heifers and thus also reflects the retention of bull's female progeny. A lower sire variance of 0.072 for stayability was estimated with the heritability estimated on the underlying scale as 0.27. This estimate is higher than the heritablities estimated for stayability by Snelling *et al.* (1995) 0.09 and 0.20; Doyle *et al.* (2000) of 0.15; Van der Westhuizen *et al.* (2001) which ranged between 0.03 and 0.08 and Silva *et al.* (2003a) with heritabilities ranging 0.11 to 0.17 for Nelore cattle. However, it corresponds to heritability estimates using threshold models by Martinez *et al.* (2002) on Hereford cattle ranging from 0.13 to 0.49. As is the case with retention, stayability will predict a component of the fertility of the female offspring of a bull, since breeders tend to cull cows that do not calve every year. The way stayability was defined, however, gave no indication of the number of calves she produced but merely gave an indication whether she was still present after a given time. This will allow for a bull with cow progeny to which the breeder is favourably disposed, to have good breeding values even though his female progeny possibly did not calve regularly, but were kept in the herd for other reasons than good fertility. However, as the production of beef becomes more and more economically and efficiency orientated, few breeders still employ this practice. If a cow is not economically efficient, most breeders will cull her.

The stayability of cows in a herd can vary from breed to breed and herd to herd depending on what criteria the breeder uses to decide whether he should keep or cull a heifer. This will determine the manner and intensity of selection for fertility traits. Brumatti *et al.* (2002) estimated the economical value of stayability as corresponding to 44% of the total economic value when developing a bio-economical model to obtain economical values of the traits used in beef cattle production.

Calf tempo is a binary trait for cows with a single parity, but becomes more continuous as the number of parities increase. It has similarities to calving rate as defined by Meyer *et al.* (1990) and Rust & Groeneveld (2002) as described in Chapter 4. Calving rate is a lifetime measure of the reproductive performance of a cow. Meyer *et al.* (1990) defined calving rate as the number of calves born divided by the number of opportunities a cow has had to calve. They estimated the heritability

for calving rate at 0.07 for Hereford, 0.11 for Angus and 0.17 for tropical cross breeds. Rust & Groeneveld (2002) defined calving rate as the number of calves born divided by the age of the cow and estimated a heritability of 0.04 using mixed model linear methodology (Chapter 4). In this study a relatively large sire variance of 0.114 was estimated for calf tempo.

Taking into account that heritability estimates for female fertility traits are often low as discussed in Chapters 2, 3 and 4, the sire variances and heritabilities estimated for retention and calf tempo were high. This may be as a result of the breed and breeding practices in the breed. *Bos indicus* breeds have on average later ages at puberty than *Bos taurus* breeds. Eler *et al.* (2004) argues that because puberty is later, genetic variability for fertility traits like heifer pregnancy rate seems to be much higher than in *Bos taurus* breeds. These findings correspond with the results of this study. The Afrikaner is an indigenous breed to South Africa and classified as *Bos africanus.* This class has much more similarities to the *Bos indicus* and Sanga breeds than to the *Bos taurus* breeds.

For this study the assumption was made that any heifer still present in the herd at an age of 18 months, was selected as a breeding heifer and mated. However, the information as to whether she was in the herd at the age of 18 months relied on a weight measurement taken at this age. For most cases the fact that she was weighed at 18 months will also mean that she was part of the heifer group initially selected for breeding purposes. Unfortunately many heifers may have been bred without being weighed. Therefore no records of such animals still being in the herd would be available at 18 month age, resulting in a loss of information.

It is possible that due to the restrictions of GFCAT (each sire and herd had to be represented in all or at least two categories per trait), data editing was too severe, leaving only offspring from sires that have produced many offspring that performed well. Also the contemporary groups were small. However, using Method R to analyse fertility traits in *Bos indicus* beef cattle, Evans *et al.* (1999), Doyle *et al.* (2000) and Eler *et al.* (2004) estimated heritabilities of similar magnitude than those estimated in this study.

Conclusion

From the three traits analysed in this study, calf tempo is the trait that probably best reflects the true fertility of the bull's female progeny, since it takes the rate at which female progeny calved between two given ages into account. It is therefore a measure of the reproductive performance of the female offspring of a bull for that time. When aiming to include calf tempo as a trait for which breeding values will be estimated in a national analysis on a routine basis, it is recommended that breeding values will be estimated for both male and female animals.

From this study it seems that utilizing GFCAT threshold models is not always the best option. The problems when using GFCAT threshold models were firstly that it is a sire model, therefore only breeding values for sires can be derived from a national genetic evaluation when the sire have reached an advance age. Eler *et al.* (2002) recommends that estimated progeny differences for the binary trait heifer pregnancy, should only be used for the selection of bulls when selecting for an improved heifer precocity because the accuracy of prediction is higher for the bulls (depending on their number of daughters). Secondly, restrictions when using GFCAT threshold models resulted in severe editing of the data. When Eler *et al*. (2004) used the weaning management of heifers as contemporary groups, they found that it lead to the exclusion of 23 % of the data due to homogenous groups. Using GFCAT result in very heavy restrictions on the structure of the data and rigorous editing must be performed on the data, losing potentially valuable information. To overcome this limitation, it can be considered to change the definition of the contemporary group so that there are fewer groups where zero variation is observed. Eler *et al.* (2004) concluded that heifer pregnancy is highly heritable, regardless of the contemporary group definition.

Another consideration can be to adjust each herd for herd-specific fixed effects. Snelling *et al.* (1996) observed differences in the magnitude of fixed effects between herds and found that genetic evaluations were different when pooled or herd-specific fixed effects were used. They proposed allowance for individual herd differences in fixed effects.

Chapter 6

Net Breeding Merit indicating retention and calving rate in a given population

Introduction

In Chapter 5, three traits associated with female reproductive efficiency were defined as threshold traits. From these traits, calf tempo seemed to be a trait that has some possibilities as indicator of female breeding potential for usage in a breeding program to improve female productivity and to assist breeders when selecting sires. A moderate to high heritability of 0.14 observed on the underlying scale for calf tempo was estimated in Chapter 5.

The disadvantage of calf tempo as defined in Chapter 5, was that only information from cows 5 years and older were used, and since a sire model GFCAT was used to analyse the data, no breeding values were available for females and young animals. In this chapter, calf tempo will be redefined as net breeding merit, an aggregate trait, describing both retention of male animals as well as the reproductive performance and retention of their female offspring. Beef breeders use failure to reproduce as a common cause for culling cows. Thus, by assuming that other culling reasons are of less importance, the ability of a cow to stay in the breeding herd may be considered as an indicative trait for female fertility. However, using retention as the only predictor of the fertility of a bull can be misleading in some instances, since some breeders give preferential treatment to those heifers from, for example, an expensive bull, heifers born from embryo transfer, or females that display specific breed characteristics very well.

A further reason for defining net breeding merit with more categories than those of calf tempo, was to utilize linear model procedures (REML). In the simulation study done by Meijering & Gianola (1985a,b), they compared ranking properties of linear (REML) and non-linear (GFCAT) methods of sire evaluation for ordered categorical responses. The endpoint measured was the Monte Carlo realized response to truncation selection upon predicted sire values. They concluded that when a linear

mixed model was required to describe variation of binary responses, GFCAT performed significantly better when heritability in the conceptual underlying scale was moderate to high, but for tetrachotomous responses no significant differences were measured between the realized responses to selection of linear vs. non-linear methods. Varona *et al.* (1999a,b) concluded in a study of calving ease in American Gelbvieh, that the threshold models had a 1% advantage for direct ability and a 3% advantage for maternal ability over the linear models when measuring the predictive ability of the different models defined with the mean square error for the distance between a deleted calving score and its prediction obtained from the remaining data. Caraviello *et al.* (2004) compared the predicting ability of genetic merit for daughter longevity of US Jersey sires between a Weibull proportional hazards model and a linear model. They concluded that the differences in predicting ability between the two methodologies were small when using a Kullback-Leibler distance measure. When analysing transformed calf survival measurements using linear, threshold and logistic sire models, Guerra *et al*. (2006) found the heritabilities estimated to be similar and posterior density distributions for all models normal.

Although a linear animal model is probably not the optimal model to use for analysis of categorical data, it is hoped to detect some sire variance that could be used to predict breeding values for net breeding merit for all the males in the herd. A further aim was to estimate sire variances for net breeding merit using linear and non-linear methodology to determine whether linear REML methods is a plausible alternative to non-linear GFCAT threshold models to improve net breeding merit genetically through selection. The repeatability of the breeding values obtained will be investigated from random split-daughter groups.

Material and Methods

Data were extracted from the INTERGIS (Integrated Registration and Genetic Information System) for the Afrikaner beef breed in South Africa. All female animals in the national Afrikaner herd, identifiable with a registered birth notification, were allocated to one of five categories according to the number of calvings she recorded as dam before the date of six years after her birth, was reached.

Redefining calf tempo as net breeding merit was done as follows. When a female animal born in the national herd never recorded the birth of a calf, she was placed in category 0. This resulted in the creation of a new category accommodating all females born into the herd that never produced a calf and were probably culled before reaching breeding age. It also included heifers that were bred, but failed to fall pregnant and produce a calf.

Thus, if a female never recorded the birth of a progeny, irrespective to the reason why, she was allocated to category 0. These animals were all included to distinguish between bulls that have consistently produced daughters that failed to stay in the herd (for genetic (reproductive) and non-genetic (breeder preference) reasons) compared to those bulls that produced daughters that calved regularly. For example, a distinction had to be made between a bull that produced 20 daughters of which 18 was retained in the herd as breeding cows resulting from good retention for whatever reason, and those that might have produced 100 daughters but only 18 were kept as breeding cows. A distinction between these bulls is only possible when all female animals born in the national herd, this is all females with registered birth notifications, is considered when categorizing the data. All heifers, still living in the national herd, but too young for breeding, were also categorized in category 0.

If a cow recorded the birth of only one calf before a date six years after her birth was reached, she was placed in category 1. This is a birth recorded at any age below six years. Whether the cow was still alive or previously culled when this date six years after her birth was reached, is not relevant. Cows younger than six years and still living in the herd, that had recorded the birth of only one calf, were also placed in category 1. Cows who had one calf, and still more opportunities on the account of not being six years old, would also be placed in category 1. Similarly, cows with two calves were placed in category 2, those with three calves in category 3 and cows with four calves in category 4 even if they had not reached six years of age.

Net breeding merit was defined similarly to calf tempo but included two more categories. The cut-off age of 5 years was extended to a cut-off date 6 years after her birth, creating additional categories in which the female progeny of a bull could be placed. As calf tempo was previously defined, no distinction was made between cows that calved twice before the age of 5 years and those that performed excellently

by calving 3 times before the age of 5 years. With the redefinition of calf tempo as net breeding merit, an extra category was created for such good performers. Also, for calf tempo, only cows that reached the age of 5 years or more at the time of the analysis were considered. This was not a requirement for net breeding merit.

Females used as embryo donors were omitted from the data. Table 6.1 gives a summary of the general statistics of the data. Only female offspring of sires older than 9 years were used to estimate the variance components, in order to give all sires equal opportunity to have female offspring present in all 5 categories. After editing, records of 18 739 Afrikaner females from 766 sires were used to estimate variance components for net breeding merit. The cut-off age of six years was chosen arbitrarily, suggesting that by the age of six years, it would be possible to establish whether a cow is a good breeding animal or not.

Table 6.1 General statistics of Afrikaner beef data used for non-linear (GFCAT) and linear (REML) analysis of net breeding merit

	Number	**Percentage (%) Selected for breeding**
No of data records	18 738	
Cat 0	8 737	
Cat 1	2 433	24
Cat 2	3 566	36
Cat 3	3 577	36
Cat 4	425	4
No of sires	766	
h*y*s levels	1 014	

h*y*s = herd*year*season concatenation

Fixed effects included were a breeder*year of birth*season (h*y*s) concatenation. Seasons were classified as season 1 (Dec - Feb), season 2 (March - May), season 3 (June - Aug) and season 4 (Sept - Nov). Genetic parameters were estimated using the GFCAT sire model set of programmes, developed by Konstantinov (1992), based on the threshold model, with support for REML-type variance component estimation derived from the methods of Gianola & Fouley (1983). All available sire relationships were taken into account.

The REML VCE4 package (Groeneveld, 1994a,b; Groeneveld & García-Cortés, 1998) was used to estimate sire variances using a REML sire model.

To determine the repeatability of the breeding value estimation, the data was divided by randomly splitting the daughters of each sire into two groups. Two more genetic analyses were performed per methodology (linear vs non-linear) in order to obtain estimates of the repeatability of the estimated breeding values.

In an attempt to account for the heterogeneous variances in the h*y*s subclasses, the effect of h*y*s was included in the linear model as either fixed or random. Hagger & Hofer (1990) concluded that non-linear models were very sensitive to a herd*year effect as either fixed or as random, but were all very similar using REML estimates.

Results

From Table 6.1 it can be seen that 46% (8 737 out of 18 738) of daughters of the 766 sires were never recorded as breeding females in the national herd or were too young to be bred at the time of the study. To a large extent the preference of breeders for specific phenotypes determine whether females are selected for breeding or not. From those that were selected for breeding (10 001 females) 24% recorded only one calf, 36% two, 36% three and 4% recorded four calves within a six year period.

The sire variances and derived heritability estimates for net breeding merit using non-linear GFCAT and linear REML sire models, are presented in Table 6.2.

Table 6.2 Sire variance components and heritability estimates of the non-linear GFCAT and linear REML VCE 4 analyses with h*y*s included as either fixed or random

	GFCAT	REML h*y*s fixed	REML h*y*s random
Sire variance	0.06	0.052±0.004	0.063±0.006
Derived heritability (h^2)	0.23	0.20	0.24
Number of equations		2704	2704

h*y*s = herd*year*season concatenation

The correlations between the sire solutions obtained from non-linear (GFCAT) and those obtained from linear (REML) models firstly with h*y*s fitted as fixed and secondly with h*y*s fitted as random, were 0.99 and 0.73, respectively.

Dempfle & Hager (1983) found that the breeding values estimated for the same sire from randomly split daughter groups by applying the same methodology, is a good criterion to rank procedures for genetic gain achievable. It will also indicate the repeatability of a trait for a given methodology. The correlations from the spilt-daughter groups estimated from the breeding values for the net breeding merit for sires from the non-linear (GFCAT) model, was very poor but for the linear models (REML) the correlations were higher for the sires estimated when h*y*s was fitted as random rather than fixed (0.46 vs. 0.61).

Discussion

The percentage of females for the Afrikaner breed that achieved the top category were small (4%) compared to other breeds where this number can be as high as 11% (Chapter 7) of females. To understand this phenomenon, it must be understood how and where the Afrikaner is bred. The Afrikaner is a hardy breed used almost exclusively for extensive farming. Breeding of heifers usually only commence later in more arid regions extending the age at first calving to later. This agrees with the observation by Martin *et al*. (1992) and Eler *et al*. (2004) that Zebu heifers reach puberty at an older age than heifers of *Bos taurus* breeds.

Figure 6.1 illustrates effects, factors and other traits that influence the measurement of net breeding merit. Factors that influence net breeding merit will be determined not only by the genetic merit of the female and her offspring for reproductive rate, but also the genetic merit of the sire. The genetic merit of the sire will in turn influence the performance of every individual female he is mated to since his genetic ability to reproduce can influence her observed performance. It is a multi factorial event where any possible malfunction or drastic change in any of the factors can have a severe effect on net breeding merit observed. For this reason, it is important for a female animal and her female offspring to have good stayability

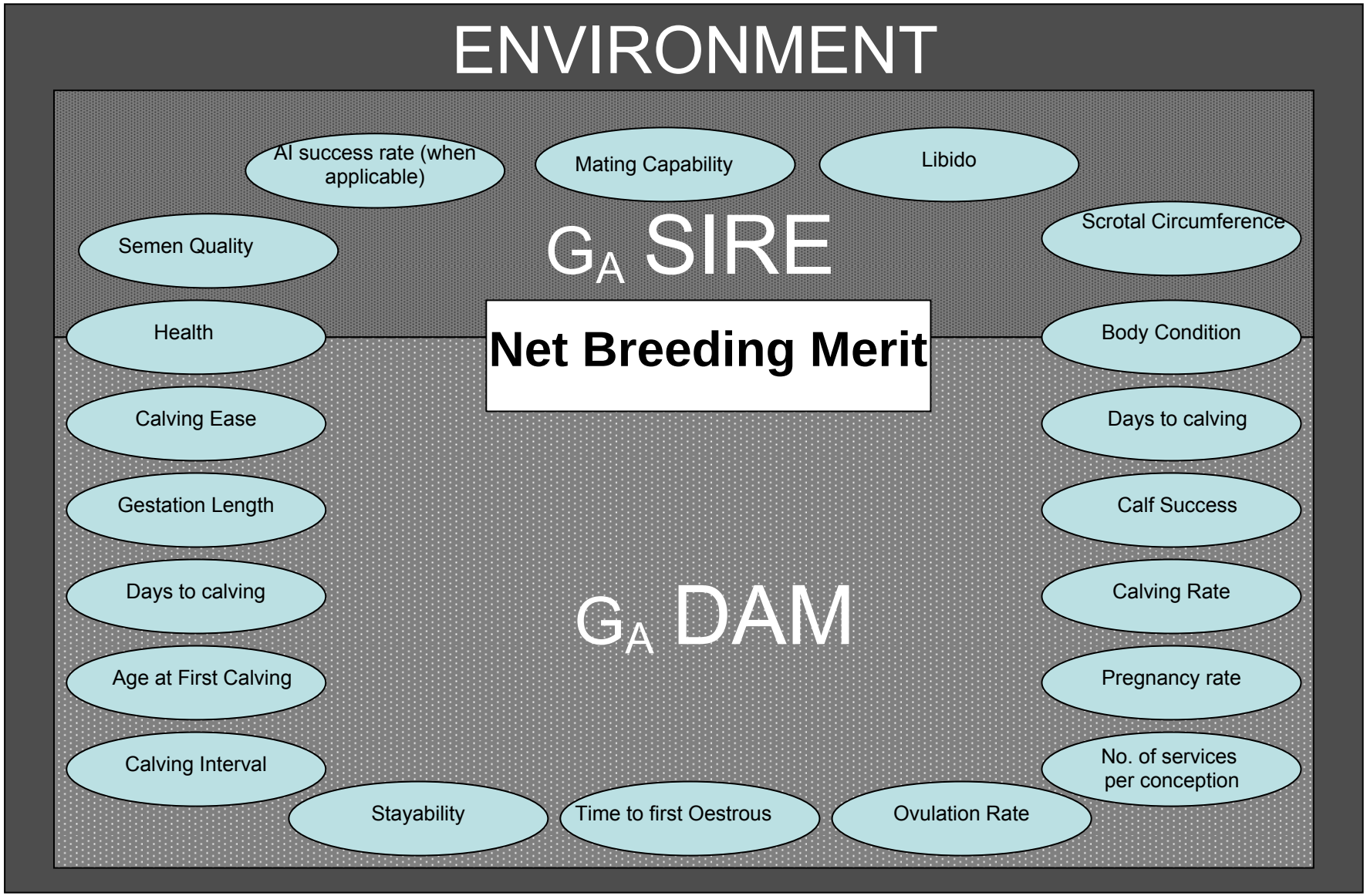

Figure 6.1 Factors influencing net breeding merit in beef cattle.

components. This should result in a more stable and accurate observation of net breeding merit.

The interaction of all the factors in the female component of net breeding merit has already been described in Figure 2.1 (Chapter 2). In Figure 6.1, additional factors such as health, semen quality, mating capability, libido, scrotal circumference and general body condition for the male component are illustrated.

Another aspect which makes the observation of net breeding merit more complex is the fact that both the male and female components do not act on a solitary basis but has an intricate interaction between them which makes the recording of a trait such as net breeding merit more complex and more sensitive to any change in a multitude of elements. It is hoped that selection intensity on the male side usually ensures that only males with acceptable health, semen quality etc. are considered.

Net breeding merit will reflect many aspects and events measured during the lifetime of a cow. Net breeding merit will reflect both component and aggregate traits. Since the environment influences all components of reproductive ability for both the sire and his female offspring, the environmental effects that include factors such as age of the animal, nutritional plane and resources, and the managerial decisions taken by the breeder, will influence net breeding merit.

Net breeding merit is not normally distributed in a given population. Other authors do, however, estimate variances using linear models for traits that have skew distributions in populations. Examples are traits such as dystocia (Meijering, 1985; Hagger & Hofer, 1990), stillbirth (Hagger & Hofer, 1990), calving ease (Table 2.1) and days to calving (Table 2.1).

Linear models are theoretically not suitable for categorical traits (Gianola & Foulley, 1983), but some simulation studies (Meijering & Gianola, 1985a) and analysis of field data (Meijering, 1985; Hagger & Hofer, 1990) suggested minor differences between sire rankings from linear and non-linear methods. When using field data, Meijering (1985) concluded that sire solutions obtained by REML and GFCAT were highly correlated (r = 0.99) for dystocia (4 categories) as well as for stillbirths (2 categories). Hagger & Hofer (1990) estimated similar correlations for dystocia and stillbirths for three beef cattle breeds, ranging from 0.97 to 0.99. In their

study, Matos *et al.* (1997) concluded that the goodness of fit of REML and non-linear models for discrete reproduction traits was similar, and with respect to prediction ability, differences between models were negligible.

In this study negligible differences in the estimated variance components were found when h*y*s was included as either fixed or random, but the solutions differed considerably. The correlation between the solutions for the two models (fixed or random) was 0.73. From the split daughter groups the results obtained showed a higher repeatability in estimation of breeding values when h*y*s was fitted as random. However, since fitting h*y*s as fixed correlated best with the solutions obtained from GFCAT, it is suggested that h*y*s should be fitted as fixed when using linear REML models.

Conclusion

As net breeding merit is currently defined, it is a composition of two traits, namely retention and female calving rate. Due to the restrictions of the South African recording system in the past, it is impossible to partition the retention information and that of calving rate of female offspring. This allows some discussion on the legitimacy of such a trait combination. However, up to date, net breeding merit is the only trait defined in South Africa that give some indication to breeders as to which bulls have or are likely to have an impact on the population in terms of retention as well as the calving rate of their daughters. For any breeder it is an added advantage to have an indication as to how 'successful' a sire is expected to be as a breeding sire in a given population. In a study of code of disposal at different parities of Large White sows, Arango *et al.* (2005) concluded that different sow removal reasons seem to operate similarly or as a closely related genetic trait associated with fitness.

Net breeding merit is a trait that estimate not only the retention of a sire's female offspring in a given population, but gives added information by taking the calving performance of a sire's female offspring into account when predicting a breeding value for that sire.

The obtained sire variances show that the trait is heritable and can therefore be improved by selection. Despite its shortcomings, the trait, as defined, give an indication of the net breeding merit or 'success' of sires in a given population. Further

investigation is needed on the application of an animal mixed model for net breeding merit. Additionally, investigation is needed on how to include data from sires younger than nine years of age as well as how to compensate females too young to have reached their full breeding potential.

Chapter 7

Estimating genetic parameters and predicting adjustment factors for net breeding merit

Introduction

In Chapter 6 net breeding merit was defined as a trait describing both the retention of the progeny of male animals as well as the reproductive rate of female offspring from those sires by categorizing the female offspring according to their reproductive performance up to the date six years after their birth. From the conclusions drawn in Chapter 6, it is a viable option to use linear animal models to estimate breeding values for net breeding merit. The aim in this chapter was to estimate genetic parameters and breeding values for net breeding merit for all animals using linear mixed animal models (REML).

The aim was further to investigate the influence of the herd and the season of calving on the expression of net breeding merit. Systematic environmental effects influence the expression of traits. The correct adjustment for age, herd and season of calving are the basis for predicting breeding values (Wilmink, 1987). In the dairy industry classification of lactation records by calving season, age at calving and herd level of production are necessary to facilitate the adjustment of records with the derivation of standard lactation curves as well as projection factors (Olori & Galesloot, 1999). Test-day records of heifers collected in early lactation standardised for age and season are of potential value for early genetic evaluation of bulls and cows for 305-day yields (Mostert *et al*., 2001). In a similar manner, a method to adjust for young females, too young to have reached the top categories for net breeding merit, is investigated by using best linear unbiased estimate (BLUE) deviations to derive adjustment factors for herd level and season of calving to predict performance for net breeding merit. Possible differences between the Afrikaner and Bonsmara breeds were investigated.

Materials and Methods

Data were extracted from the INTERGIS (Integrated Registration and Genetic Information System) for the indigenous Afrikaner and Bonsmara beef breeds of South Africa. As described in Chapter 6, all female animals were allocated to one of five categories according to the number of calves produced (recorded at birth of the calf) before a date of six years after the birth of an individual female is reached. Females used as embryo donors were omitted from the data.

Data of sires with more than 50 female offspring were selected for both breeds. To reduce the size of the data set available for the Bonsmara breed to limit computational difficulties, only herds with more than 500 recorded births were selected for genetic parameter estimation. All available animal relationships were considered. Table 7.1 gives a summary of the general statistics of the Afrikaner and Bonsmara data used for the mixed linear model analyses.

The GLM procedure of SAS was used to determine the best operational model for both breeds for genetic parameter and breeding value estimation. Fixed effects included were a herd * year of birth * season of birth concatenation. Seasons were classified as season 1 (Dec - Feb), season 2 (March - May), season 3 (June - Aug) and season 4 (Sept - Nov). The age of sires (in days) were included in the model as linear and quadratic co-variables for the Afrikaner breed and as a linear co-variable for the Bonsmara breed. This was done to accommodate the varying ages of sires in the population and to compensate young males that have not yet bred females old enough to reach the top categories.

Estimation of genetic parameters was done for both the Afrikaner and Bonsmara breeds on the complete data set (after editing) using linear animal models.

After estimation of genetic parameters on the complete data sets, the data for both breeds were divided. The data sets were divided into four data subsets representing females of different age class groups. Four age class groups were identified. These groups included three, four, five and six year olds.

Table 7.1 General statistics of data used, after editing, for analyses of net breeding merit using mixed linear animal models for the Afrikaner and Bonsmara breeds

	Animal Model	
	Afrikaner	**Bonsmara**
No of data records	39 063	30 363
No of animals in pedigree	124 671	61 416
Cat 0	20 762 (53%)	14 009 (46%)
Cat 1	6 865 (17%)	3 302 (11%)
Cat 2	6 862 (17%)	3 326 (11%)
Cat 3	4112 (10%)	6 387 (21%)
Cat 4	462 (1.2%)	3 339 (11%)
No of sires	525	213
h*y*s levels	6 755	3 525

h*y*s = herd*year*season concatenation

To select the three-year age group of females, the calving record of a cow was categorised when she reached the age of three and any further calving records of the cow was ignored. In this way, she was categorised on her performance up to the age of three years. The same procedure was followed to select four and five year old cow groups. For the last group, the six year olds, all information on all females represented in the data were used to categorise the cows.

Four more VCE4 REML analyses per breed were done, one for each of the data sets representing the different female age class groups. The aim of these analyses was to obtain the BLUEs for each herd and each season for each breed, respectively. Therefore herd and season were both individually fitted as fixed effects in these models and not as h*y*s concatenation. The BLUEs obtained from these analyses were then compared over age group classes for herd and season of calving for the Afrikaner and Bonsmara, respectively. The possibility to use the deviations of the BLUEs for the different age groups to compensate females too young to have reached the top category, was investigated.

Results and Discussion

From Table 7.1 it can be seen that there is a vast difference in the breeding pattern of the two breeds. For the Afrikaner 53% (20 762 out of 39 063) daughters of the 525 sires were never selected as breeding females in the national Afrikaner herd. From those that were selected to breed 17% (6 865 females) calved only once before they were culled, 17% twice, 10% three times and 1.2% four times. The respective percentages for the Bonsmara breed are 46%, 11%, 11%, 21% and 11%. Breeding for Afrikaner heifers usually commences at a weight of 320kg-340kg, and this weight is generally reached at the age of two and a half years of age. This is in agreement with the results by Martin *et al*. (1992), who found that Zebu heifers historically reach puberty at an older age. Another reason for the low percentage observed in the top category for the Afrikaner can probably be due to the fact that Afrikaner cows are known to show lactation anoestrous, especially so between first and second calving (Madjuda, 1997).

Summaries of the results from the animal model genetic parameter estimation and breeding value estimation for both the Afrikaner and Bonsmara beef breeds are presented in Table 7.2. The heritabilities estimated for the Afrikaner and Bonsmara for net breeding merit were 0.078 and 0.109, respectively. These estimates are moderate when compared to heritability estimates of other aggregate traits and component traits that consider the calving rate of female animals. From the literature heritability estimates for calving rate vary between 0.02 and 0.17 when open cows are taken into consideration, for length of productive life heritability estimates are between 0.05 and 0.15, for days to calving between 0.05 and 0.13 and for calving interval heritability estimates range between 0.01 and 0.07 (Table 2.1). In Chapter 6 a higher heritability estimate of 0.20 were estimated for the Afrikaner beef breed. However, the data was severely selected in such a manner that only included female offspring of sires older than nine years, thus excluding information from offspring of younger sires.

Table 7.2 Genetic parameters estimated for net breeding merit from animal model VCE4 REML analyses

	Afrikaner	Bonsmara
V_e	0.85±0.01	1.79±0.01
V_a	0.07±0.01	0.22±0.01
h^2	0.078	0.109

After dividing the two data sets in four subsets, each according to the ages of the cows, four more REML analyses were done for each breed. The deviations of the BLUEs of the four analyses per breed were compared for every herd and each season. The results are presented in Figures 7.1 and 7.2 for different herds for the Afrikaner and Bonsmara, respectively.

Variation in the BLUE deviations occurred between all age class groups for the Afrikaner (Figure 7.1), whereas for the Bonsmara, the variation between the BLUE deviations for the 3 year old age group seems greater than the variation in the other age group classes (Figure 7.2). BLUE deviations for herd fixed effect in the three year old age group for the Afrikaner breed ranged between -0.2874 and 0.3566 and for the other age class groups between -0.7487 and 0.0922. BLUE deviations for herd fixed effect in the three year old age group for the Bonsmara breed, however, ranged between -0.0467 and 0.1886 and for the other age class groups between -0.0136 and 0.1064.

The magnitude of the BLUE deviations for fixed effect of the herd performance level for net breeding merit is greater in the Afrikaner breed than in the Bonsmara breed. For the Afrikaner the same amount of variation due to the herd effect occurs for all three age class groups. The difference between the highest and lowest BLUE deviation for herd for all three age classes are more or less 0.75 of a category point. For the Bonsmara breed it seems that there is less influence due to herd performance level on net breeding merit in age classes 4, 5 and 6 than in the 3 year age class group. The deviation between the 3 year old age group is approximately 0.14 and for the 4 to 6 year age classes 0.05 of a category point, respectively.

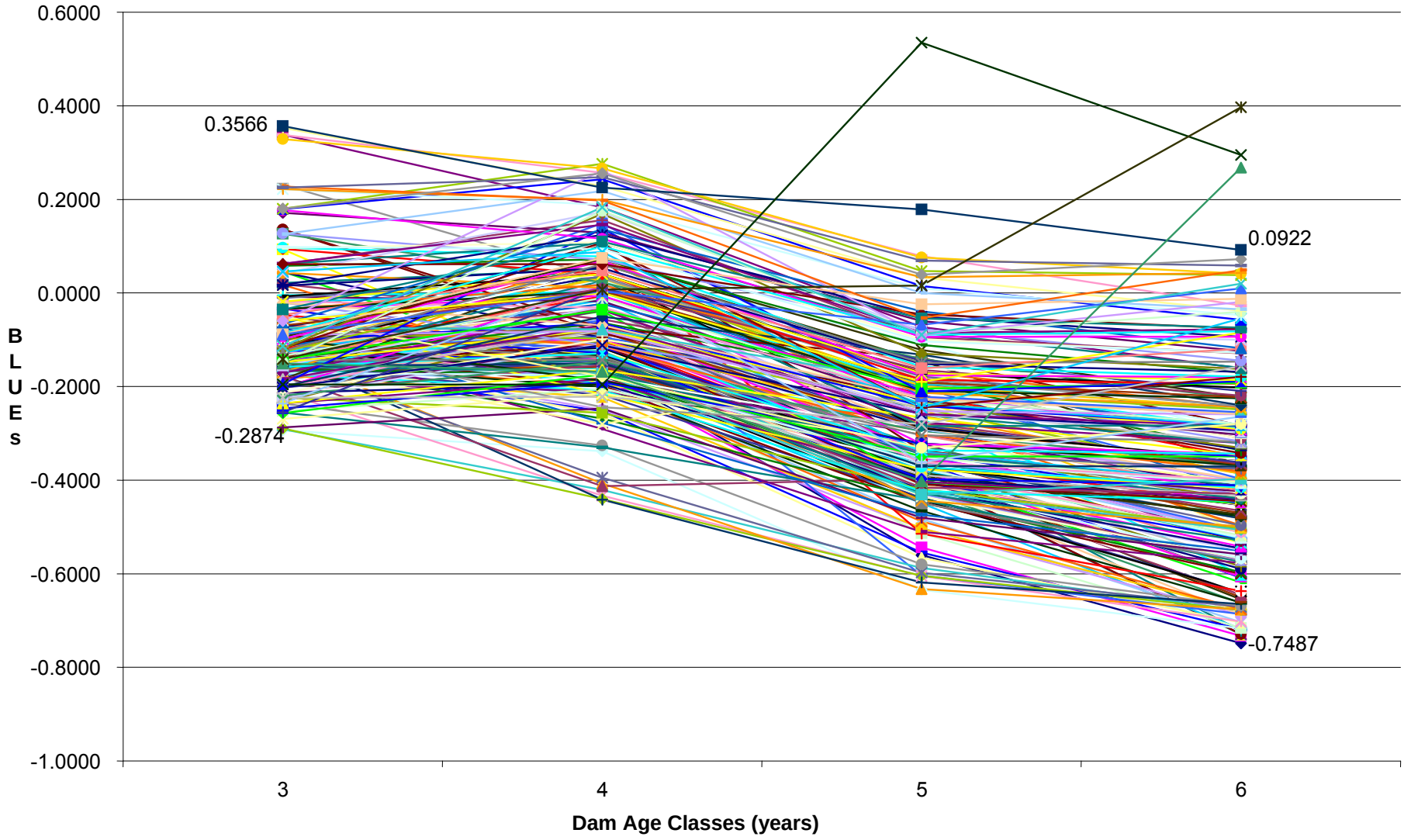

Figure 7.1 Standard performance curve due to herd level for different age classes for the Afrikaner breed.

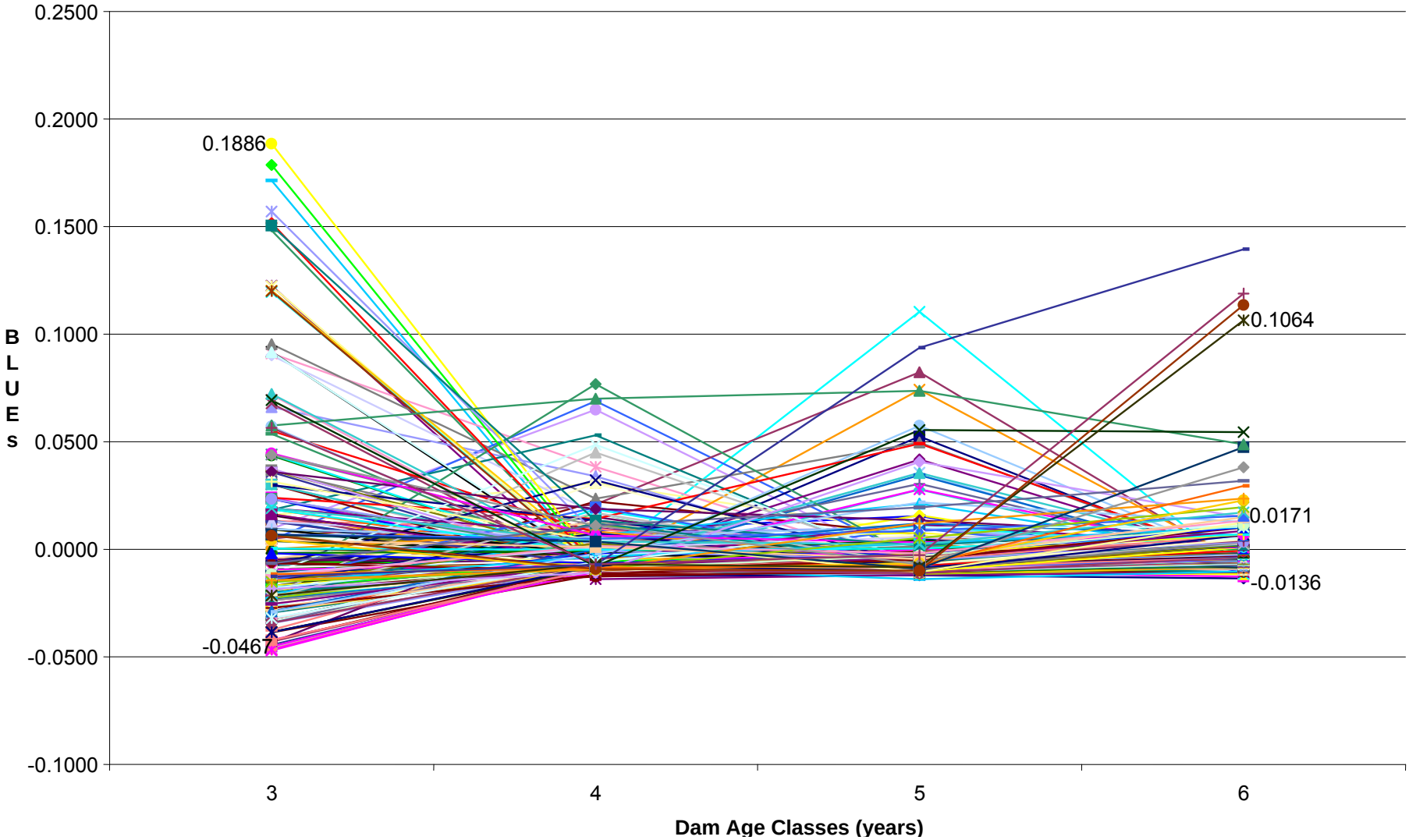

Figure 7.2 Standard performance curve due to herd level for different age classes for the Bonsmara breed.

One possible reason for the larger herd deviation in the 3 year old age group for the Bonsmara, could be the act that their reproductive performance is apparently influenced much more distinctly by the environment at a younger age than at later ages.

After adjustments according to the standardised curve for performance level of herd were made on the phenotype (observations) for net breeding merit, the impact of the BLUE adjustments on the data structure is clearly visible and is illustrated in Figures 7.3 and 7.4 for the Afrikaner breed and in Figures 7.5 and 7.6 for the Bonsmara breed, respectively.

Deviations due to the fixed effect of season are presented in Figures 7.7 and 7.8 for the Afrikaner and Bonsmara breeds, respectively. The deviations of the BLUEs for both breeds are small, and range between 0.13 between season 1 (Dec - Feb) and season 3 (June - Aug) for the 5 year old age class of the Afrikaner breed and 0.01 for both breeds in all seasons. It is concluded that due to the small magnitude of the BLUE deviations, no adjustments to the phenotype needs to be done regarding the standardised curve due to season performance level.

Conclusion

From the results, it seems likely that mixed animal model methodology will give accurate estimates of the genetic variance existing for net breeding merit. In Chapter 6 a higher heritability estimate of approximately 0.20 were estimated for the Afrikaner breed, while a value of 0.08 was estimated in this chapter when information of offspring from younger sires were included (current study). In Chapter 6, the data were selected in such a way that only female offspring of sires older than nine years were considered. This probably accounts for the difference in heritability estimates for net breeding merit of Afrikaner cattle. Even though the estimate was lower, the variances estimated in this chapter indicate genetic variation for net breeding merit in the Afrikaner breed and that improvement can be achieved through selection.

For the Bonsmara, heritability was estimated as 0.11 for net breeding merit, indicating genetic variation for net breeding merit in the Bonsmara breed and that, through selection, improvement can be achieved for this trait.

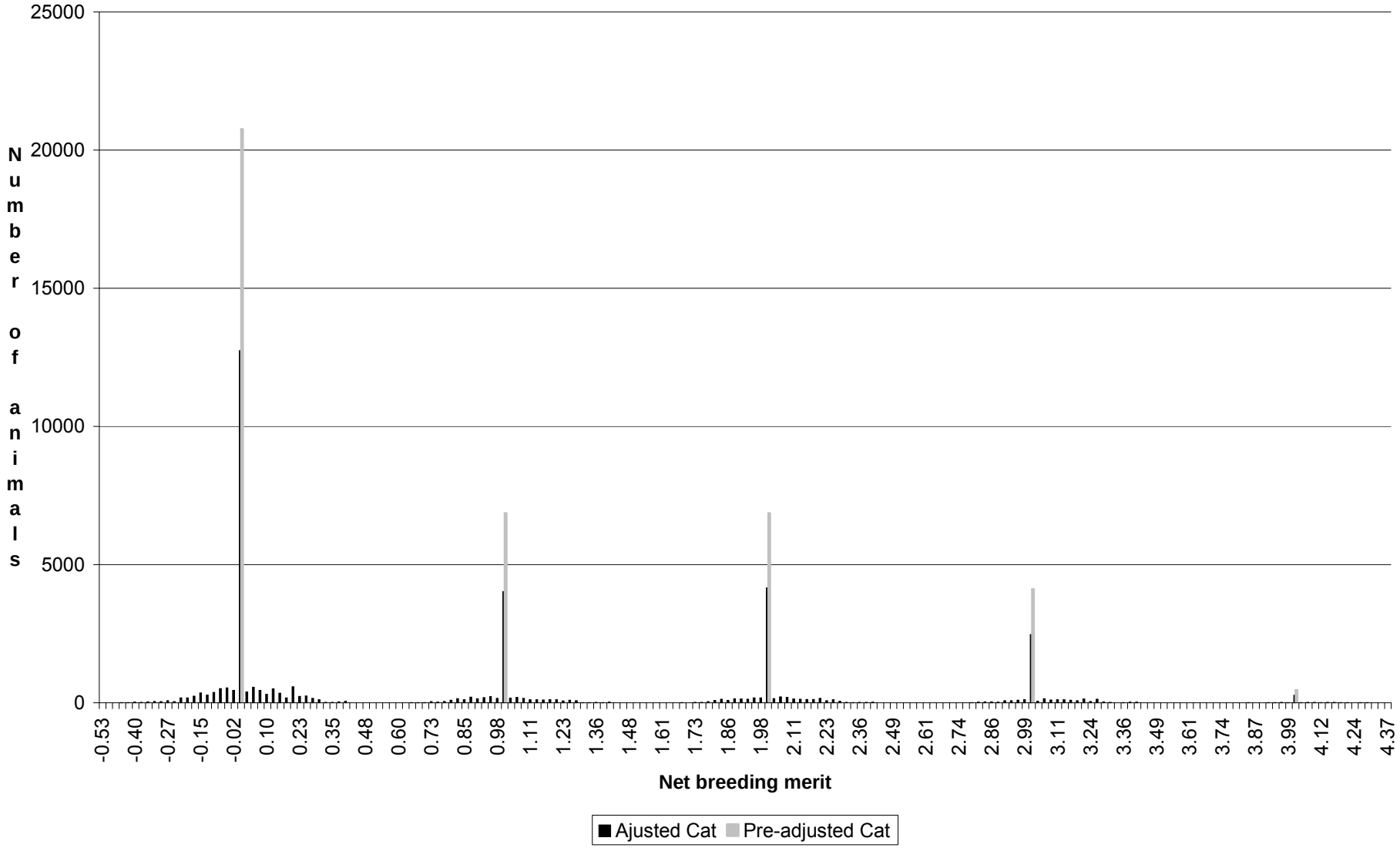

Figure 7.3 Frequency of observations for net breeding merit for all categories for the Afrikaner breed before and after adjustment using the standardised herd performance level curve.

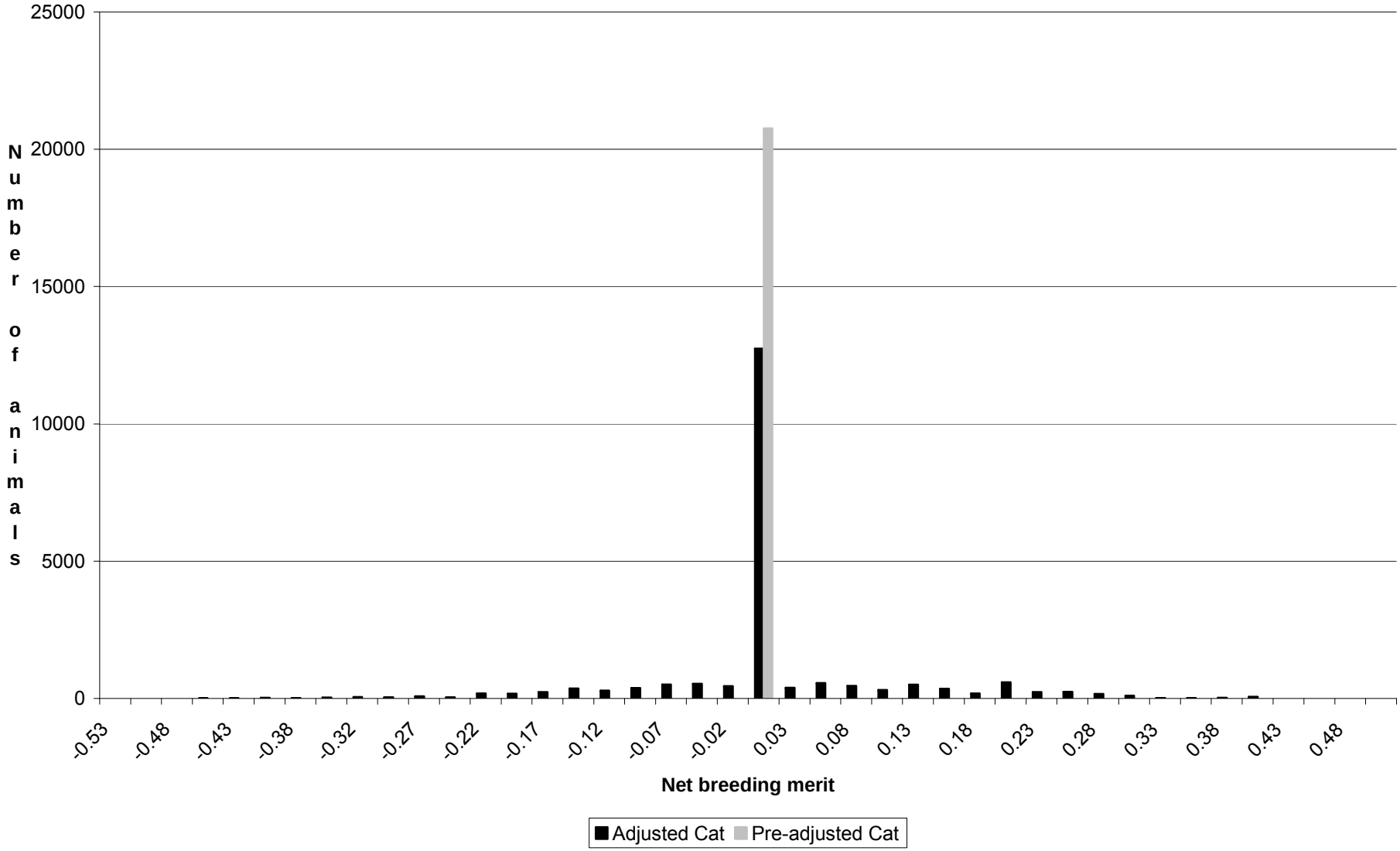

Figure 7.4 Frequency of observations for net breeding merit for category 0 for the Afrikaner breed before and after adjustment using the standardised herd performance level curve.

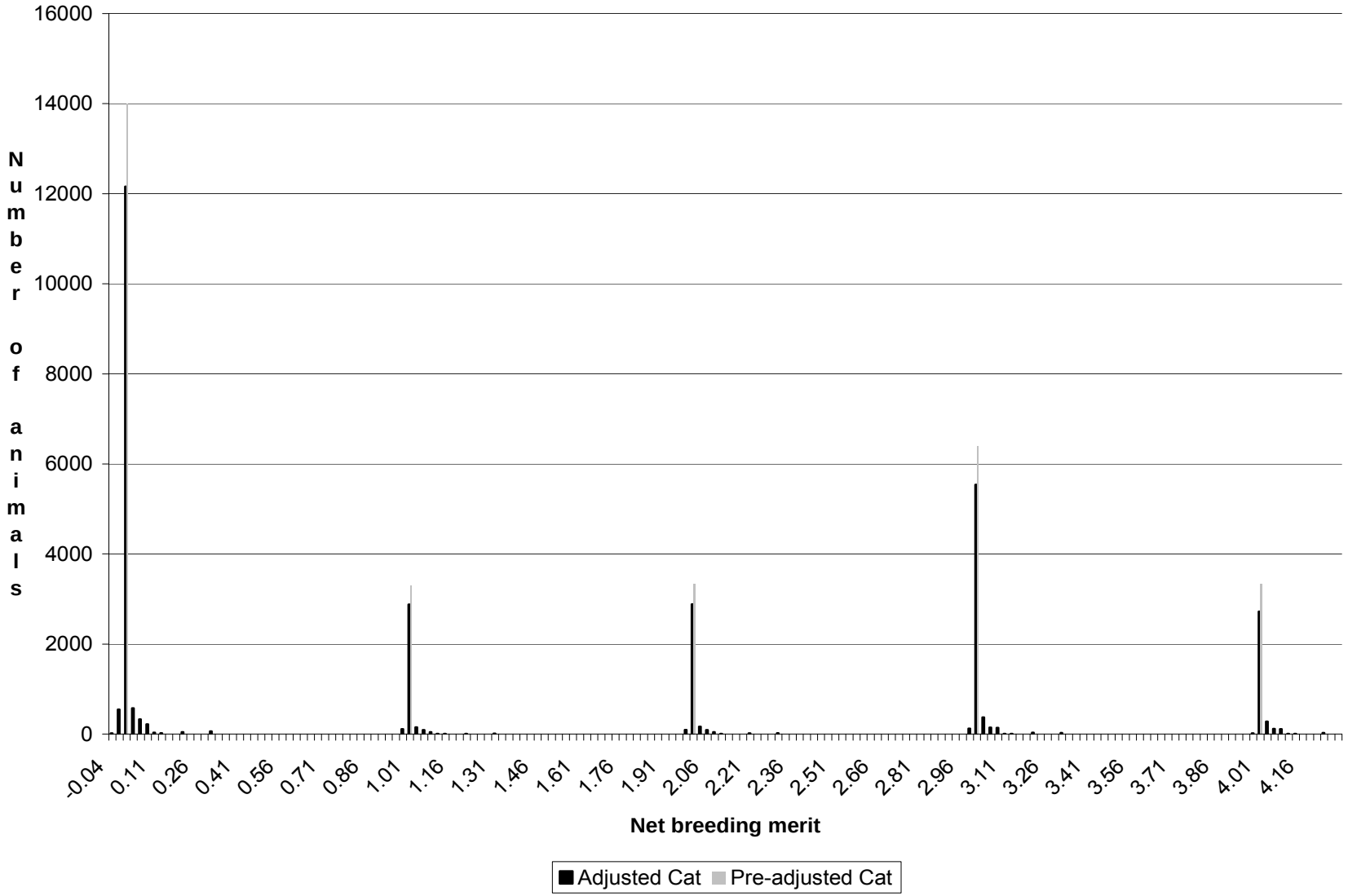

Figure 7.5 Frequency of observations for net breeding merit for all categories for the Bonsmara breed before and after adjustment using the standardised herd performance level curve.

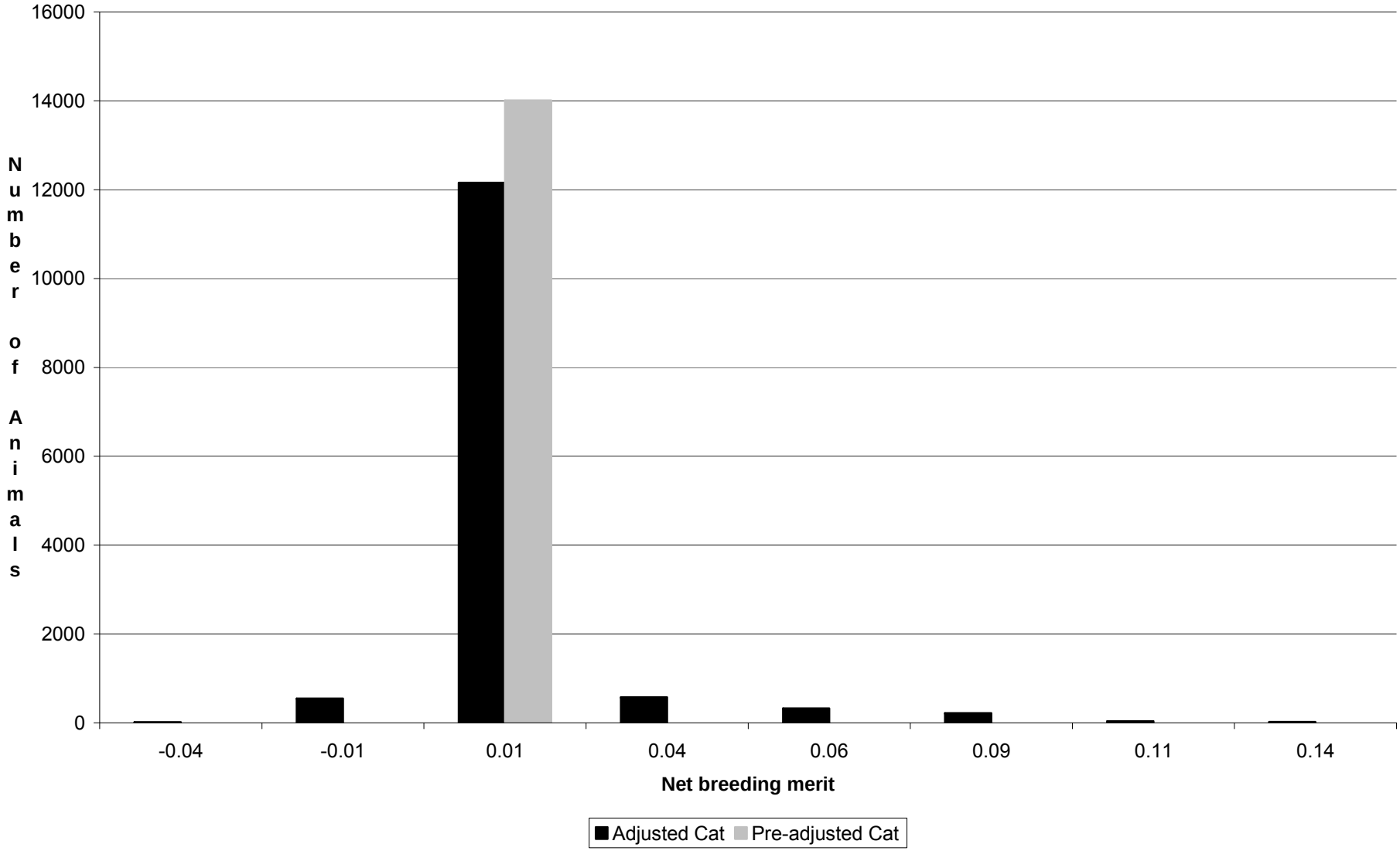

Figure 7.6 Frequency of observations for net breeding merit for category 0 for the Bonsmara breed before and after adjustment using the standardised herd performance level curve.

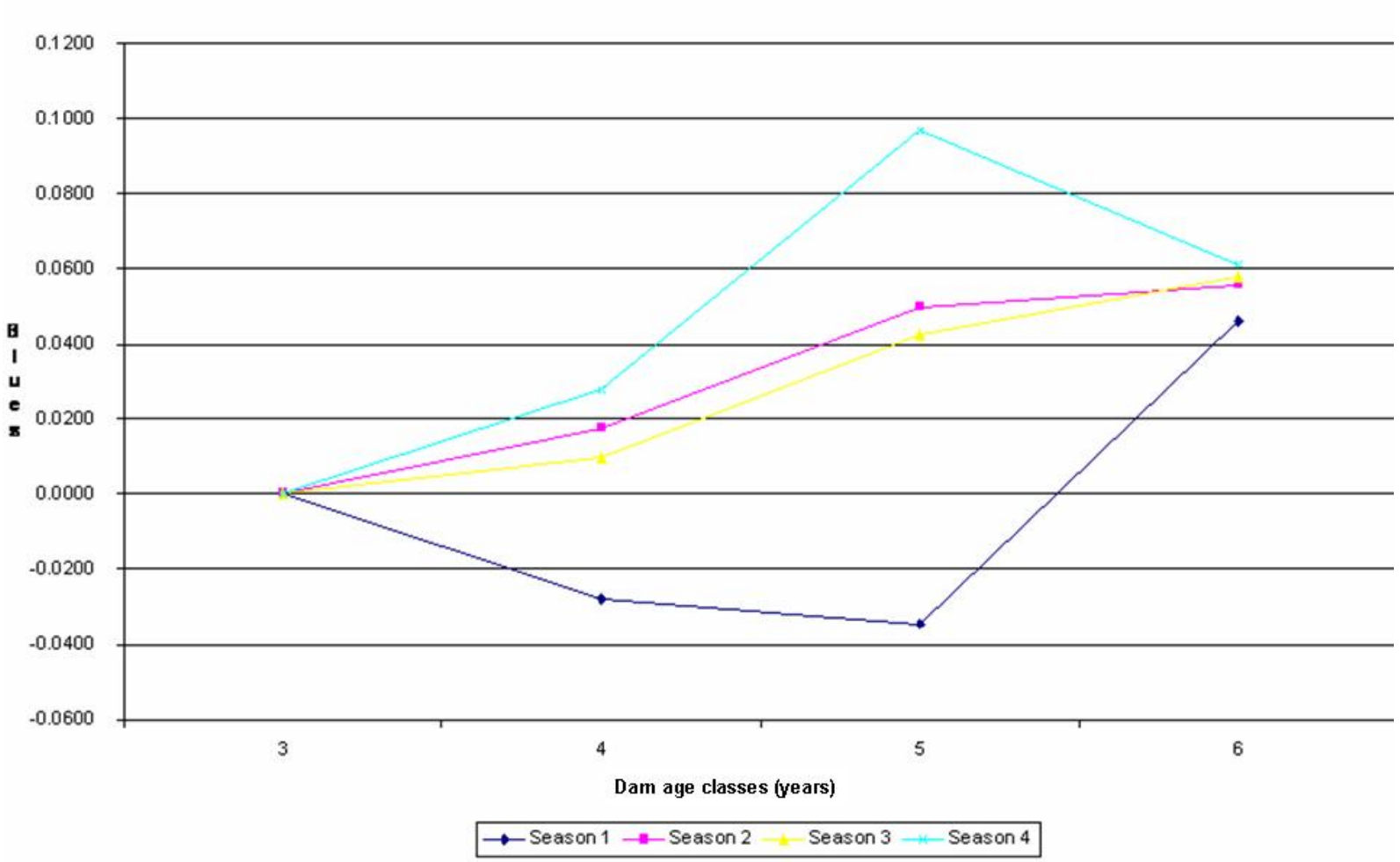

Figure 7.7 Deviations of BLUEs for fixed effect season in different age classes for the Afrikaner breed.

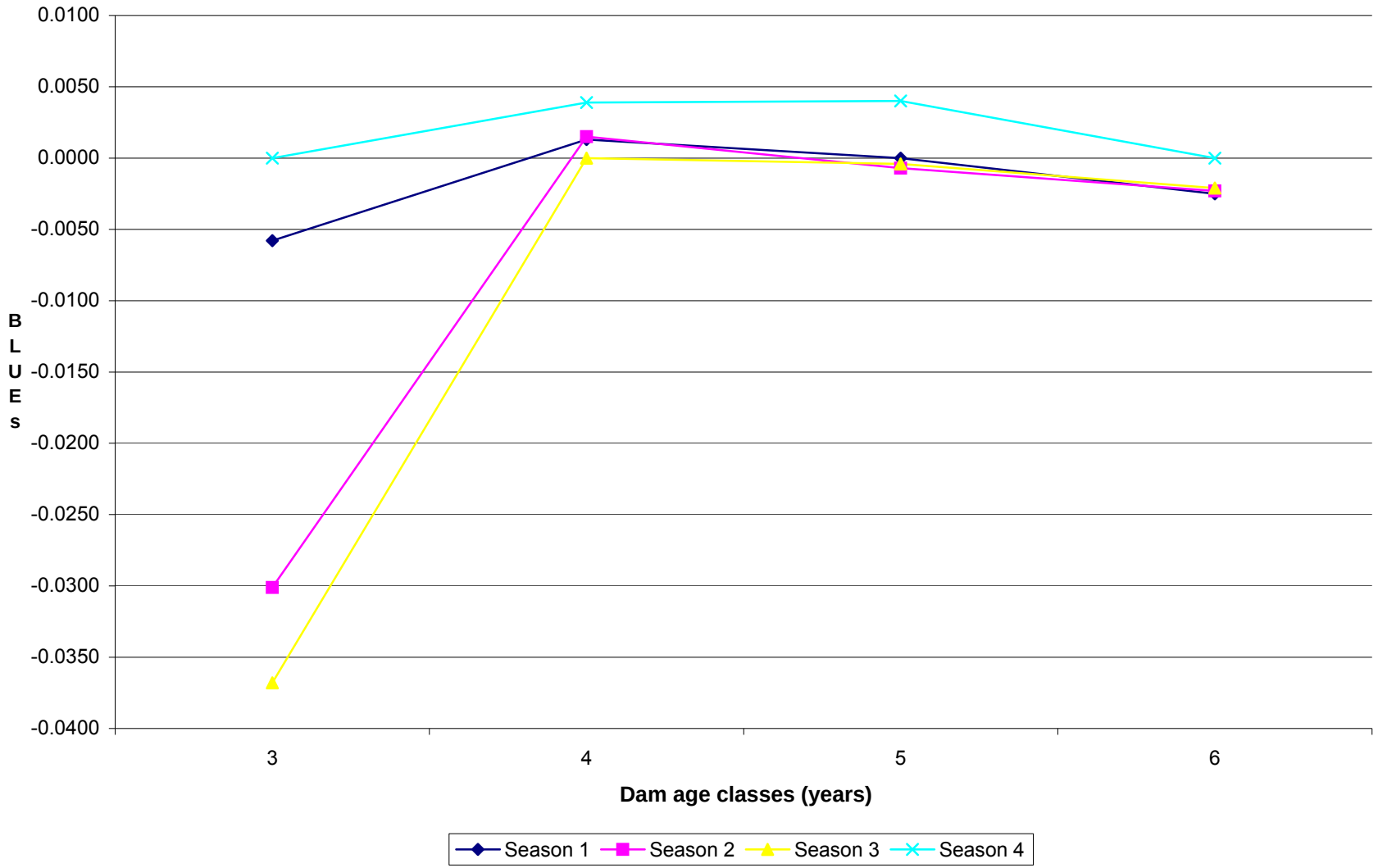

Figure 7.8 Deviations of BLUEs for fixed effect season in different age classes for the Bonsmara breed.

The results from this study clearly indicated that variation due to herd fixed effect occur in females of both breeds. Where this variation is present in all age classes for the Afrikaner, for the Bonsmara breed the herd effect differences seem greater in the 3 year age group than for older age class groups. The magnitude of the differences also seems smaller for the Bonsmara than for the Afrikaner. The reason why the herd effect is greater in the Afrikaner than in the Bonsmara can possibly be due to the differences between *Bos taurus* and Sanga breeds. Eler *et al.* (2002; 2004) suggest that females from *Bos indicus* breeds reach puberty at later ages because they were not selected for sexual precocity in the past, and, therefore greater variation exist in these breeds for early fertility. Early fertility is one of the component traits influencing net breeding merit. The effect of the managerial system as well as the effect of the resource a female is kept on (fixed effect of herd), will thus probably influence the expression of net breeding merit substantially. The Afrikaner is an indigenous breed to South Africa and classified as *Bos africanus,* which is similar to the *Bos indicus* and Sanga breeds. Thus, for the Afrikaner breed, the fixed effect of herd has major effect on the expression of net breeding merit. A further possible explanation for the larger variation due to herd effects for the Afrikaner, can be attributed to the large differences in the environments where the Afrikaner is farmed in South Africa.

It is suggested that the standardised curve for herd performance level derived from BLUE deviations can be used to adjust the phenotypic values of animals younger than the date six years after their birth. By using the standardised curve of herd production level for each age group, a prediction can be made of the category an animal should be placed in. Each phenotype of these animals will thus be adjusted with the deviation prediction due to its specific herd, creating more categories, moving to a more continuous variable within each category. It is the aim that by doing this, the comparison between older and younger animals in the population to be more just.

Chapter 8

General Conclusion

Probably the most important factor influencing the economic viability of beef cattle production is successful reproduction. Reproductive success is essential for beef cattle enterprise to be profitable. Hansen (2006) has shown that a one percent change in reproductive performance will generate up to 3 times more return on investment for cow/calf operators when compared to a one percent change in production and/or product quality. Displayed fertility in a beef herd is a combination of female and male fertility as well as proper managerial regimes. If one of these factors is sub-standard, the overall fertility of the cow herd will be compromised (Hansen, 2006).

The aim of this study was to search for a quantifiable measure that describe the genetic merit of female beef animals to assist breeders when making selection decisions by the provision of estimated breeding values. This measure must be simple and inexpensive to record in any beef herd irrespective of the herd's managerial strategy. For beef cattle, as is the case in most other domesticated livestock species, traits linked to reproduction are generally the factors that contribute most to overall efficiency and productivity. Reproduction efficiency should ultimately play a huge role in whether the breeding merit of an animal as parent will be good or not.

In the cow, reproduction is a complicated process that is subject to varying effects at different stages of the female reproductive life cycle that interact with or influence each other. Normal reproduction of a cow involves the synchronization and interaction of many physiological events. The successful occurrence of all these events is further influenced by the environment. Female and male components of reproduction do not act on a solitary basis, but has an intricate interaction between them. This makes the quantification of reproduction efficiency in beef cattle females even more complex and sensitive to any change in a multitude of factors. Failure of

any of the genetic, environmental or hormonal mechanisms will result in suboptimal reproduction.

The environment and resources available to a breeder and his animals usually determine which traits can be measured and recorded in a specific herd. In this study, many approaches to improve female fertility in beef cattle are investigated. Some of the traits are easy to record at no extra cost to the breeder, while some traits are difficult and costly to measure and record and need the assistance of an experienced professional.

The intensity of management of the breeding enterprise can also influence which traits will be recorded since some traits need close observation at regular time intervals to obtain accurate measurements. These recordings will not be possible in semi- or extensive managerial breeding systems. It will only be possible to measure them in intensive systems where close observation of the animals is possible.

All traits described in this study, to a greater or lesser degree, describe aspects of the reproductive performance of beef cattle females. Most of the traits, the component traits, are measured at a specific event in the lifetime of a cow while aggregate traits consider the lifetime production of a cow. These traits are measured over many events that take place in the lifetime of a cow.

Many of the traits considered in the previous chapters, showed constraints when analyzing the data with regards to methodology and inadequacies in data structure. For these traits, there is a need for guidelines to standardize the recording practice to obtain meaningful information. Data should be recorded with for a specific purpose. Very often, animal breeders utilize data recorded for other purposes and use it to quantify female fertility even though the data recording was never intended for that purpose. This often creates difficulties when defining contemporary groups. Groups of animals weighed together will not necessarily be animals that were mated together as a contemporary group. Thus, when data are recorded for a purpose other than for the recording of reproduction measurements, crucial data are often amiss, resulting in some generalities and assumptions. For example, when females are culled from a herd, often no record is taken concerning her reproductive status when she was culled. However, for any measure of lifetime reproduction merit of female animals in a herd, these recordings are extremely important. A similar limitation is often

experienced when data of natural mating and AI are indistinguishable and all AI dates as well as joining dates are not recorded.

It is clear that measuring and then quantifying female reproduction efficiency merit, is difficult. If a breeder is interested in improving the genetic merit of his breeding herd for reproductive merit, numerous options are discussed in the previous chapters. All of the traits have varying merits as indicators of reproductive efficiency. Some of the traits discussed, indicate serious constrains in the existing South African system for beef cattle recording, but given other recording systems might be good indicators of female reproductive ability.

In this study, traits were investigated when they complied with the aims described above i.e. simple and inexpensive recording in all intensity levels. Two component traits, age at first calving and days to calving were investigated in Chapter 3. Both traits could quantify breeding merit of females in a national herd. In Chapter 4, two aggregate traits were considered. Calving rate was defined different from similar traits previously defined in the literature. This was done to ensure that the aim of the study, i.e. simple and inexpensive recording in all intensity levels could be achieved. For all these traits genetic variance of varying levels were observed rendering them fit as traits that could be used in national evaluations indicating female breeding merit.

Four new categorical traits were defined either for the first time or defined in a way that differed from the way they were described previously in the literature. The traits were defined as retention, stayability, calf tempo and net breeding merit.

Taking into account that heritability estimates for female fertility traits are often low as discussed in Chapters 2, 3 and 4, the sire variances and heritabilities estimated for retention and calf tempo were high and that for stayability intermediate. From these traits, calf tempo probably reflects the reproduction merit of the bull's female progeny the best, since it takes the rate at which female progeny calved between two given ages into account. It is simple and inexpensive to record and can be used in a breeding program to improve female productivity and assist breeders when selecting sires.

Further investigation into calf tempo, led to a redefinition as net breeding merit. A low to moderate heritability was estimated for net breeding merit. Net breeding

merit is a trait that estimate not only the retention of a sire's female offspring in a population, but gives added information by taking the calving performance of a sire's female offspring into account when predicting a breeding value for that sire. The obtained sire variances indicate that the trait is heritable and would thus respond to selection. The trait gives an indication of the net breeding merit or 'success' of sires in a given population. For any beef breeder it will be of great value to have an indication as to which sires are more likely to produce female offspring that are retained in the herd and are likely to maintain a good calving rate.

A comprehensive investigation was done into different ways of explaining and describing female reproduction efficiency merit for beef cattle females. Some suggestions were given as to what traits are suitable in varying resource environments and differing managerial systems. The onus lies with each breeding society to select for one or more than one of these traits so that genetic improvement of reproductive efficiency in the female population can be made through selection. Data should be recorded specifically for the purpose of improving reproduction merit to achieve this.

Some recommendations can be made when data are recorded for of measuring and quantifying reproductive merit in beef cattle females.

1. Eliminate selective recording.
2. Data recorded for other purposes should not be extrapolated to attempt to quantify female fertility traits.
3. Entry and exit dates and reasons for exit from herds must be recorded.
4. The pregnancy status of all females in the herd should be known and recorded at all events.
5. All joining and AI dates should be known.
6. Proper distinction should be made between natural mating and AI data in herds where both are being used.
7. Contemporary groupings should be defined clearly and recorded.

During this investigation, some areas were exposed that needs further investigation.

1. The existence of a possible genotype x environmental interaction for the trait age at first calving.

2. Analysing age at first calving using a Weibull analysis
3. An adequate and fair penalty system for open cows when analysing days to calving records.
4. When analysing categorical traits calving rate, stayability and calf tempo, a method to measure improvement must be investigated.
5. Investigate the relative value of retention vs. reproductive efficiency in the trait net breeding merit.
6. Continue investigating the feasibility of using standard deviation curves to make adjustments to net breeding merit data.
7. Investigate standard deviation curves for net breeding merit for all beef breeds.

When scientists investigate the reproductive efficiency of beef cattle it is a means to contribute to the well-being of society. By finding simple, inexpensive and effective ways of increasing the efficiency of reproduction, the financial gain of the beef enterprise as well as the supply of food to society is increased. The complete micro economic environment surrounding the beef enterprise will eventually profit from an improved production without additional input. Genetic gain, especially improvement in reproductive efficiency creates more efficient beef herds.

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